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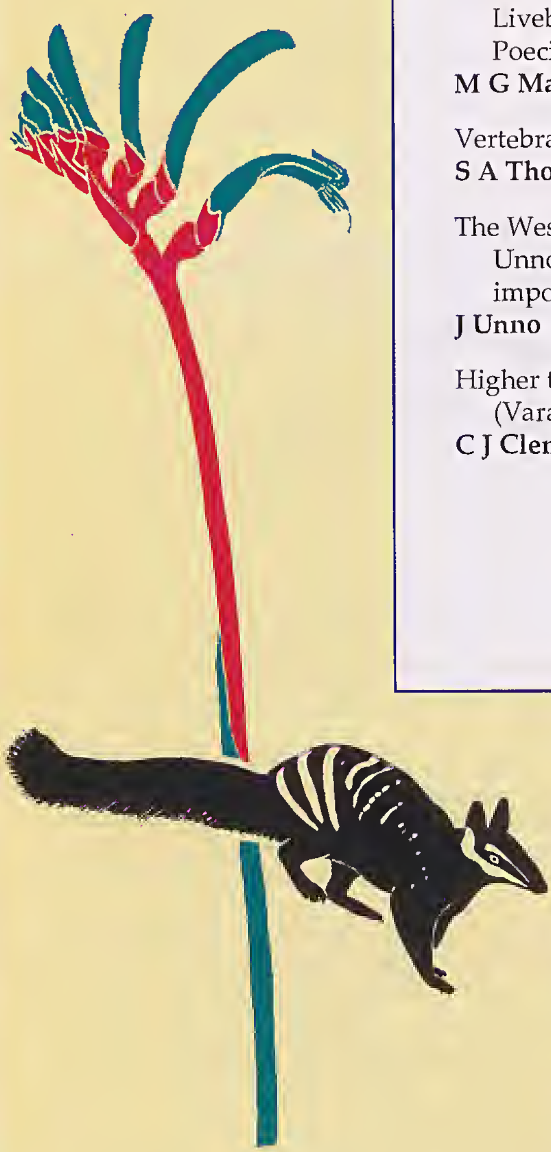
CONTENTS



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The Journal of the Royal Society of Western Australia was first published in 1915. Its circulation exceeds 600 copies. Nearly 100 of these are distributed to institutions or societies elsewhere in Australia. A further 200 copies circulate to more than 40 countries. The Society also has over 350 personal members, most of whom are scientists working in Western Australia (see website http://www.ecu.edu.au/pa/rswa). The Journal is indexed and abstracted internationally.

Cover design: The four subjects symbolize the diversity of sciences embraced by the Royal Society of Western Australia. Mangles' kangaroo paw (*Anigozanthos manglesii*) and the numbat (*Myrmecobius fasciatus*) are the floral and faunal emblems of Western Australia, and stromatolites are of particular significance in Western Australian geology (artwork: Dr Jan Taylor). The Gogo Fish (*Mcnamaraspis kaprios*) is the fossil emblem of Western Australia (artwork: Danielle West after an original by John Long).

Biota of the Mandora System, Western Australia: – Mammals

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Abstract

The Mandora System is an internationally important wetland situated on the boundary of two bioregions belonging to different biological provinces. Its biota was poorly known before a survey of selected taxa in 1999. The recorded mammal fauna is not particularly diverse (16 native species comprising eight marsupials, four bats and four rodents). It included species from both provinces but the Eremaean was better represented than the Torresian. Highly saline surfaces had fewer species than either loamy or sandy surfaces. Other notable features included the presence of some species at or close to the known limits of their distributions and the presence of two 'critical weight range' (CWR) species within the study area. Two more CWR species are reported from nearby in habitats that are widespread in the study area.

Keywords: Mammals, Eremaean and Torresian bioregions, saline soils, loams, desert dunefields.

Introduction

The Mandora Paleo-river is a now-occluded system that once drained the south-east Kimberley and adjacent parts of the Northern Territory across the Great Sandy Desert to the Indian Ocean at the (present-day) Eighty-mile Beach (van de Graaff *et al.* 1977; Wyrwoll *et al.* 1986). Its mouth was associated with a marine embayment which has been cut off from the sea by the formation of coastal dunes (K-H Wyrwoll pers. com.). Today, inland of the coastal dunes, saline sediments and loamy soils are flanked by red, aeolian dune fields. They extend to about 80 km east of the present coastline. Biogeographically, the red dune fields belong to the (Eremaean province) Great Sandy Desert bioregion (GSD) and the coastal dunes support a narrow strip of the (Torresian province) Dampierland bioregion (DL) that parallels the coast along most of the Eighty-mile Beach. The saline sediments comprise an intrusion of DL the into the GSD (Fig. 2).

The area is part of the Ramsar-registered Eighty Mile Beach Wetland of International Importance (Anon 1999; DCLM 2003). Its outstanding features include inland occurrences of the mangrove tree *Avicennia marina* (Avicenniaceae) and mangrove fern *Acrostichum speciosum* (Pteridaceae). Fresh-water mound springs occur in the midst of saline landscapes. They support forests of *Melaleuca leucadendron* (Myrtaceae), and/or swampy areas containing beds of *A. speciosum*, the 'bulrush' *Typha domingensis* (Typhaceae), and the small wetland/riparian tree *Sesbania formosa* (Fabaceae). Ephemeral lakes sometimes support up to 500,000 waterbirds and many species breed there when conditions are suitable (Halse *et al.* 2005). Cattle, *Bos taurus* and to a lesser extent camels, *Camelus dromedarius* and donkeys, *Equus asinus* are affecting conservation values, particularly biota associated with the mound springs. Current tenure is pastoral lease (Anna Plains Station) but conversion to a conservation reserve is proposed (G. Graham pers. com.).

Given the area's location at the boundary of the Eremaean and Torresian provinces and the significance of its natural features, remarkably little is known of its biota except water birds. In 1983 NMcK collected bats and some terrestrial vertebrates. In 1999, a multi-disciplinary team including ANS and PK investigated the flora, vertebrate fauna and some aquatic invertebrate groups and documented the results in Graham (1999) but they are not formally published or readily available. In 2001, PK obtained some additional mammal records. This paper presents the information on mammals obtained on those three occasions. Anticipating publication of results for other groups in a similar format, we provide site data in some detail.

Methods

Study Area

The study area is at about 19° 45' S, 121° 25' E, some 40 km inland of the Eighty Mile Beach, Western Australia (WA) Fig. 1. It experiences a semi-arid monsoonal climate with hot summers and warm winters. Rainfall is erratic but predominantly occurs in summer (January to March) and the area is affected by frequent cyclones (typically, several per decade). Median annual rainfall is 326 mm at Mandora Station and 360 mm at Anna Plains Station (about 60 km west and north of the study area

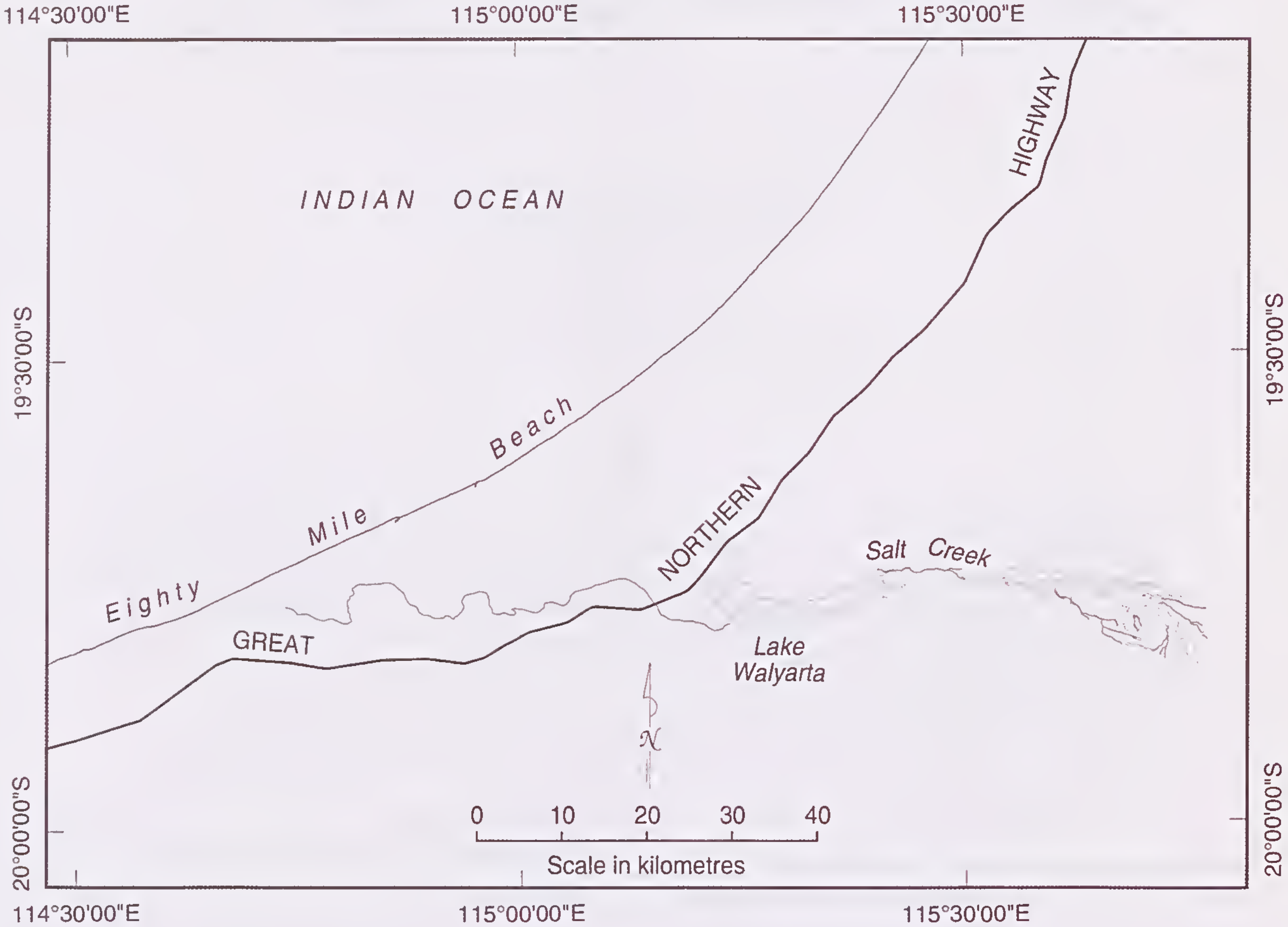

Figure 1. General location of the study area.

respectively). Mean monthly maximum temperatures range from ~30°C in July to ~39°C in January. Wyrwoll *et al.* (1986, 1992) described the Holocene climates and their role in the hydrological and geomorphological development of the system.

A large ephemeral lake, Lake Walyarta, near the western end of the former marine embayment is linked eastward (*i.e.* inland) with a series of smaller ephemeral lakes by Salt Creek, a blind channel that holds permanent salt water, and is fringed by *Avicennia marina* trees. The valley floor comprises saline clays and loams underlain by secondary calcretes that are evident in the bed of Salt Creek and outcrop as small ridges in some low-lying areas. Soils become progressively less saline, more loamy and then sandier as the valley sides rise towards the flanking, red dune fields.

The study area is situated to the south of Salt Creek. A typical north-south section runs from bare saline clays, through halophytic 'samphire' communities (predominantly, *Halosarcia* spp., Chenopodiaceae), then swards of *Sporobolus virginicus* (Poaceae) on saline clays. Above them, less saline clays support sparse shrublands over perennial and annual grasses including *Aristida* sp., *[1] *Cenchrus ciliaris* and *Eragrostis* sp. Hummock grass (*Triodia* sp.) occurs on raised areas including calcrete outcrops. In places, thickets of *Acacia ampliceps* (Mimosaceae) and several *Melaleuca* spp. (Myrtaceae) add a structurally important tall shrub layer to the vegetation. Higher on the valley sides, hummock grasses become more prominent and the shrub flora becomes more diverse. The boundary with red sandy dunes and swales of the GSD is usually well defined and corresponds with significant changes in vegetation structure and floristic composition but some integration occurs where shallow sands partly cover marginal DL surfaces.

In addition to Salt Creek, *Avicennia marina* occurs in some low-lying areas that are subject to inundation as well as some linear depressions in areas dominated by swards of *S. virginicus.* Mound springs and associated swamps of fresh to brackish water occur throughout the system. Those supporting *Melaleuca leucadendron* forests tend to have thickets of A. *ampliceps* near their margins and areas of open water but sparse, if any, understoreys (*e.g.* Eil Eil Spring). Others have dense beds of *Typha domingensis* or A. *speciosum* in a 'moat' of fresh water and emergent *S. formosa* over dense thickets of A. *ampliceps* on peaty soils of a central mound (*e.g.* Fern Spring).

Sampling

Sample site characteristics are shown in Table 1. Most sites were located on DL surfaces associated with the

[1] * is used throughout to indicate exotic taxa.

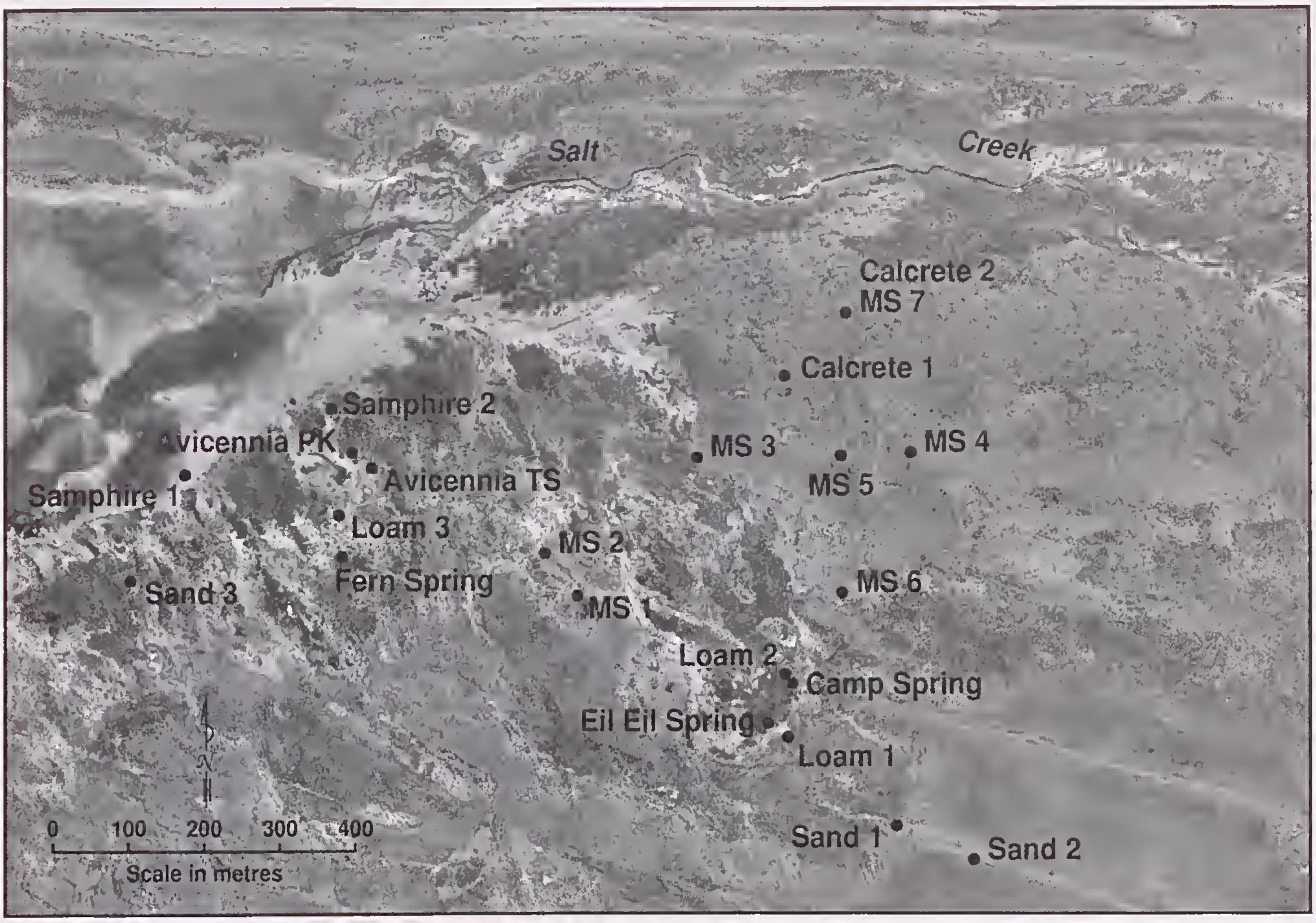

Figure 2. Sample site locations superimposed on a satellite image of the study area to show the juxtaposition of Great Sandy Desert and Dampierland bioregional systems. The former is typified by linear dune systems clearly visible to the north and southeast of the area and the latter by the complex array of surfaces through the centre of the image.

former marine embayment but red sand surfaces of the GSD were also sampled.

From 12–17 August 1983, NMcK sampled bats by spotlight-shooting and mist-netting and terrestrial mammals with pit traps and modified metal break-back rat-traps (Table 2). From 12–21 October 1999, vertebrate fauna and flora were sampled systematically in ten quadrats positioned along the altitudinal catena from sometimes-inundated samphires on the saline lake margin to red dunes. Both pit traps and medium-sized Elliott traps were used. Where shallow water tables prevented the use of pit traps, additional sites were trapped less rigorously (informally) with Elliott traps, to provide some sampling of major habitat types not represented in quadrats (Table 2). In both years, pit traps were made from 60 cm lengths of 125 mm diameter white PVC tubing seated on aluminium flywire floors. In 1983, they were set in lines of (usually) six pits along 50 m drift fences made from 30 cm wide strips of flywire. In 1999, five randomly-placed pairs were set in each quadrat. Five-metre drift fences were erected between and to each side of each pair. Besides site-based trapping, incidental sightings, tracks and scats, were recorded where they added to knowledge of the occurrence or distribution of mammals in the area. Nomenclature follows How *et al.* 2001. Distributional information refers only to Western Australia. All specimens have been deposited in the Western Australian Museum.

Results

Sixteen native mammals were recorded as extant in the study area (Tables 3 and 4): eight marsupials (four dasyurids, three macropods and a bandicoot), four bats and four rodents. There were also seven introduced species (three carnivores, including the dingo, *Canis lupus dingo*, three large herbivores and a rodent). Numbers of each taxon trapped at sample sites were too low for quantitative site comparisons. Therefore, results are presented for the three distinctive substrate types, highly saline soils and loams of DL and red sands of GSD (Table 4). Although numbers are still too low for meaningful quantitative analysis, the results are indicative and consistent with previously recorded habitat preferences (*e.g.* van Dyck & Strahan 2008).

Native mammals were least diverse (3 species) and, amongst species amenable to trapping, least abundant (4 animals) on highly saline substrates. They were a dasyurid, a large macropod and a rodent. All three individuals of the dasyurid, *S. macroura*, were taken in halophytic low shrublands (samphire); the macropod, *M. rufus*, was present in all major habitats and is capable of moving between them at will within the study area. However only one of five *P. desertor* trapped in the study area was from this surface-type. It was trapped in a sward of the halophytic grass, *S. virginicus*; the others were taken on red sands (3) and a loamy surface (1). In

Table 1

Location and summary of geo-physical and vegetation attributes of trapped sites listed from high to low landscape settings. Sites prefixed 'MS' were sampled in 1983 and the remainder in 1999. GSD = Great Sandy Desert bioregion, DL = Dampierland bioregion.

Site name and type	Co-ordinates	Landscape position	Landscape setting and soil	Bioregion and Vegetation
MS 06 Informal	19°46'54" 121°27'20"	High.	Dune. Red sand. "A" horizon weak to absent. Humus and charcoal visible <10 cm.	GSD. Diverse shrubs over hummock grass.
Sand 1 Quadrat	19°48'35" 121°27'44"	High.	Dune and adjacent swale margin. Red sand. "A" horizon weak to absent. Humus visible at surface but fading < 10 cm.	GSD. Diverse shrubs over hummock grass.
Sand 2 Quadrat	19°48'50" 121°28'19"	High.	Dune and adjacent swale margin. Red sand. "A" horizon weak to absent. Humus and charcoal visible <10 cm.	GSD. Diverse shrubs over hummock grass.
MS 07 Informal	19°44'53" 121°27'23"	High.	Swale. Red sand. "A" horizon weak to absent. Humus and charcoal visible >10 cm.	GSD. Sparse, low trees and diverse shrubs over hummock grass. Regenerating after fire
MS 08 Informal	19°42'06" 121°28'25"	High.	Swale. Red sand. "A" horizon weak to absent. Humus and charcoal visible >10 cm.	GSD. Sparse, low trees and diverse shrubs over hummock grass.
Loam 1 Quadrat	19°47'56" 121°26'55"	High/ Moderate	Red sand, in places overlying loamy sand. Latter uniform to 60 cm. No obvious "A" horizon.	DL/GSD interface. Low acacia thickets and diverse shrubs with hummock grass.
MS 03 Informal	19°45'55" 121°26'15"	High/ Moderate	Near interface of aeolian red sand and loamy soils. Medium to fine brown sand <30 cm over clay-loams. "A" horizon weak to absent.	DL (near GSD interface). Sparse, low trees and sparse shrubs over hummock grass.
Sand 3 Quadrat	19°46'46" 121°21'57"	High/ Moderate	Isolated dune overlying loamy soils. Red sand (dune) and paler sandy clay (remaining surface). "A" horizon weak to absent on both. Humus/charcoal not noted.	GSD/DL interface. Sparse, low trees and diverse shrubs over hummock grass (on dune) or tussock grasses (heavily trampled by cattle) on remainder.
Loam 2 Quadrat	19°47'29" 121°26'54"	Moderate.	Pallid pink-grey, somewhat saline sandy-loam or loam, Damp below 30 cm.	DL. Scattered thickets of *Acacia ampliceps* and *Melaleuca* sp. shrubs over annual and perennial grasses.
Camp Spring Informal	19° 47' 33" 121° 26'57"	Moderate	Outer margin of mound spring 'moat'. Grey, somewhat saline loam or clay-loam. "A" horizon not noted.	DL. Mid-dense thicket of *A. ampliceps* with sparse understory. Rushes at water's edge.
Eil Eil Spring Informal	19°47'50" 121°26'46"	Moderate	Margin of mound spring. Grey, somewhat saline loam or clay-loam ("A" horizon not noted) adjacent to litter over deep peaty soil.	DL. Thicket of *Melaleuca* sp and *A. ampliceps* adjacent to forest of *M. leucadendron* with little/no understory
MS 02 Informal	19°46'54" 121°25'05"	Moderate/ Low	Evaporite on saline, greyish sandy silt and clay. "A" horizon not noted.	DL. *Acacia ampliceps* over halophytic shrubs, sub-shrubs and grass.
MS 04 Informal	19°45'54" 121°27'52"	Moderate/ Low.	Shallow, fine silty sand and clay over calcrete. "A" horizon not noted.	DL. Halophytic low shrubs and tussock grasses.
MS 01 Informal	19°40'53" 121°25'20"	Low	Evaporite on saline, greyish sandy silt and clay. "A" horizon not noted.	DL. Halophytic shrubs, sub-shrubs and grass.
Calcrete 1 Quadrat	19°44'53" 121°27'23"	Low.	Cracking evaporite crust over pallid grey loam. Calcrete pan (<50 cm) over crustose red sand and calcrete nodules (> 50cm). "A" horizon not noted.	DL. Halophytic low shrubs and tussock grasses
Calcrete 2 Quadrat	19°45'20" 121°26'55"	Low	Shallow soils between calcrete ridges. Cracking evaporite crust over pallid grey loam. Calcrete pan (<50 cm) over crustose red sand and calcrete nodules (> 50cm). "A" horizon not noted.	DL. Halophytic low shrubs and tussock grasses.
MS 05 Informal	19°45'55" 121°27'20"	Low	Shallow soils between calcrete ridges. Shallow, saline clay, grey silt and fine sand. "A" horizon not noted.	DL. Halophytic low shrubs and tussock grasses.
Fern Spring Informal	19°46'36" 121°23' 33"	Low/ Very low	Mound spring with freshwater 'moat'. Centre with thick litter grading into peat. Surrounded by saline clays with no observed "A" horizon.	DL. Central thicket of *Sesbania formosa/A. ampliceps*. Dense beds of *Typha domingensis/Acrostichum speciosum* in wetted perimeter and sward of *Sporobolus virginicus* beyond.

Table 1 (cont.)

Site name and type	Co-ordinates	Landscape position	Landscape setting and soil	Bioregion and Vegetation
Loam 3 Quadrat	19°46'18" 121°23'32"	Low/ Very low	Saline evaporite crust breaking to powdery surface over grey sandy-loam to10 cm, over pallid damp clay. "A" horizon not noted.	DL. Sward of the halophytic grass, *S. virginicus*
Avicennia TS Informal	19°45'58" 121°23'47"	Low/ Very low	Blind channel incised into deep, saline clay. No observed "A" horizon.	DL. Low forest to thicket of *Avicennia marina* on channel margins and sward of *S. virginicus* on adjacent plane.
Avicennia PK Informal	19°45;51" 121°23'38"	Low/ Very low	Blind channel incised into deep, saline clay. No observed "A" horizon.	DL. Low forest to thicket of A. *marina* on channel margins and sward of *S. virginicus* on adjacent plane.
Samphire 1 Quadrat	19°46'00" 121°22'22"	Very low.	Lake margin. Ridged, saline evaporite crust over damp, dark clay <5 cm over pallid clay. Releasing free water at 50 cm. No observed "A" horizon.	DL. Samphire at margin of lakebed. Indications of inundation in recent months.
Samphire 2 Quadrat	19°45'32" 121°23'29"	Very low.	Lake margin. Ridged saline evaporite crust over damp sandy clay. Hardpan at 30 cm over pale brown-grey clay to 40cm, over pallid clay releasing free water at 60 cm. No observed "A" horizon.	DL. Samphire at margin of lakebed. Inundated in recent months (dried algae draped over drowned samphire stems).

Table 2

Summary of trap effort. Numbers in parenthesis show the number of traps used and number of nights trapping respectively. BB = Modified break-back trap.

Site Name	Site Type	Dates	Elliott Trap Nights	Pit Trap Nights	BB Trap Nights
Sand 1	Quadrat	1999 October	225 (25x9)	90 (10x9)	0
Sand 2	Quadrat	1999 October	225 (25x9)	90 (10x9)	0
Sand 3	Quadrat	1999 October	175 (25x7)	70 (10x7)	0
Loam 1	Quadrat	1999 October	225 (25x9)	90 (10x9)	0
Loam 2	Quadrat	1999 October	225 (25x9)	90 (10x9)	0
Loam 3	Quadrat	1999 October	200 (25x8)	80 (10x8)	0
Calcrete 1	Quadrat	1999 October	225 (25x5)	90 (10x9)	0
Calcrete 2	Quadrat	1999 October	200 (25x8)	80 (10x8)	0
Samphire 1 (E)	Quadrat	1999 October	200 (25x8)	80 (10x8)	0
Samphire 2 (W)	Quadrat	1999 October	175 (25x7)	70 (10x8)	0
Fern Spring	Informal	1999 October	200 (50x4)	0	0
Avicennia TS	Informal	1999 October	100 (25x4)	0	0
Avicennia PK	Informal	1999 October	100 (25x4)	0	0
Camp Spring	Informal	1999 October	100 (25x4)	0	0
Eil Eil Spring	Informal	1999 October	100 (25x4)	0	0
Total 1999			2675	830	0
MS 01	Informal	1983 August	0	30 (6x5)	10 (2x5)
MS 02	Informal	1983 August	0	30 (6x5)	10 (2x5)
MS 03	Informal	1983 August	0	35 (7x5)	20 (4x5)
MS 04	Informal	1983 August	0	0	60 (12x5)
MS 05	Informal	1983 August	0	0	60 (12x5)
MS 06	Informal	1983 August	0	30 (6x5)	20 (4x5)
MS 07	Informal	1983 August	0	30 (6x5)	20 (4x5)
MS 08	Informal	1983 August	0	30 (6x5)	20 (4x5)
Total 1983			0	185	220

Table 3

Mammals recorded from the study area. Numbers handled are shown in square brackets and voucher collection numbers in round brackets (those prefixed F&W are (former) Department of Fisheries and Wildlife field numbers and those prefixed M are Western Australian Museum registration numbers).

Family	Species	Notes
Dasyuridae	*Planigale maculata* Long-tailed Planigale.	**Oct. 1999:** Fern Spring [1] (M51586). Identification confirmed genetically (Cooper *et al.* 2001).
	Planigale sp. Undescribed Planigale	**Oct. 1999:** Loam 2 [1] (M51581). Female with developed pouch. Identification confirmed genetically (Cooper *et al.* 2001). A widespread species in the Pilbara.
	Sminthopsis macroura Stripe-faced Dunnart	**Aug. 1983:** MS 02 [1] (FW2027). Male. **Oct. 1999:** Samphire 2 [2] (M51580, -99). Female with developed pouch and a male.
	Sminthopsis youngsoni Lesser Hairy-footed Dunnart	**Aug. 1983:** MS 03 [2] (FW2029, -33). Females with pouch young. **Oct. 1999:** Sand 3 [1] (M51567). Juvenile.
Peremelidae	*Macrotis lagotis* Bilby	**Oct. 1999:** Sand 1. Several recent burrows and fresh tracks.
Macropodidae	*Macropus agilis* Agile Wallaby	**Oct. 1999:** Eil Eil and Little Eil Eil Springs. Sight records. **Sep. 2001:** Loam 2, Calcrete 2, Eil Eil Spring, Little Eil Eil Spring, Grant's Spring (near Sand 3), Fern Spring. Sight records.
	Macropus robustus Euro	**Sep. 2001:** Eil Eil Spring and Salt Creek. Sight records. Apparently not common.
	Macropus rufus Red Kangaroo	**Aug. 1983:** MS 04; fresh tracks presumed to be this species. **Oct. 1999:** Sand 2, Sand 3, Loam 2, Fern Spring, Stockyard Spring, PK Avicennia. Sight records. Tracks and droppings of large macropods (probably this species) were ubiquitous but not abundant. **Sep. 2001:** Fern Spring, Grants Spring, Lake Walyarta. Sight records, including animals grazing at night on the margins of Lake Walyarta.
Pteropodidae	*Pteropus* sp. Flying Fox	**Oct. 1999:** Eil Eil Spring. Sight record. Overhead at dusk.
Emballonuridae	*Saccolaimus flaviventris* Yellow-bellied Sheathtail-bat	**Aug. 1983:** Eil Eil Spring [1] (M51581). Found dead under paper bark tree (*M. leucadendron*) with hollow spout. Another seen flying over paperbarks at same site on the same date.
Molossidae	*Chaerephon jobensis* Northern Freetail-bat.	**Aug. 1983:** Eil Eil Spring. Recorded flying over paperbarks (*M. leucadendron*).
Vespertilionidae	**Nyctophilus geoffroyi* Lesser Long-eared Bat.	**Oct. 1999:** Eil Eil Spring [1] (M51562). Mist-netted over water.
Muridae	**Mus domesticus* House Mouse.	**Oct. 1999:** Eil Eil Spring [4] (M51555, -61, -78, -79), Fern Spring [25] (M51559, -63, -64, -68, -71,-84, -85, -87, -89, -95), Loam 1 [1] (no voucher), PK Avicennia [11] (M51556, -57, -75, -77, -90, -93,-97), Samphire 2 [1] (M51560), 'TS Avicennia' [6] (M51565, -72, -74, -94, -96). Common in swamps and halophytic vegetation, particularly dense swards of *S. virginicus.* More released from these sites without being recorded. Adults in all reproductive phases and juveniles.
	Notomys alexis Spinifex Hopping-mouse.	**Oct. 1999:** Sand 1 [3] (M51558), Sand 3 [1]. Two pregnant females. **Sep. 2001:** Sand 2 [1]. Apparently not common at the time.
	Pseudomys desertor Desert Mouse.	**Oct. 1999:** Sand 1 [1] (M51583), Sand 2 [2] (M51601, -02), Loam 2 [1] (M51604), TS Avicennia [1] (M51566).
	Pseudomys hermannsburgensis Sandy Inland Mouse.	**Aug. 1983:** MS 07 [2] (FW2031, -32), MS 08 [1] (FW2035). **Oct. 1999:** Calcrete 1 [4] (M51600).
	Pseudomys nanus Western Chestnut Mouse	**Oct. 1999:** Sand 1 [1] (M51582), Loam 2 [1] (M51603).
Canidae	**Canis lupus dingo* Dingo	**Aug. 1983** Salt Creek, dunes north of Salt Creek, calcrete area south of Salt Creek. Tracks. **Sep. 2001:** Calcrete 2, Grant Spring. Tracks. (The population may include domestic dog hybrids.)
	**Vulpes vulpes* European Red Fox	**Oct. 1999:** Sand 1, Sand 2 and Loam 1. Tracks. **Sep. 2001:** Calcrete 2 and Eil Eil Spring. Tracks.
Felidae	**Felis catus* Feral Cat	**Aug. 1983:** Tracks on a red sand dune. **Oct. 1999:** Sand 1, Sand 3, Calcrete 2, Loam 1, Grant Spring, north of Salt Creek. Tracks, scats, one sight record and one old skull. A scat contained arthropods and an agamid lizard.

Table 3 (cont.)

Family	Species	Notes
Bovidae	**Bos taurus* Cattle	**Oct. 1999:** All sites except Sand 1 and Sand 2. Tracks and two sight records. Tracks were most abundant on loam surfaces and around springs. Large numbers watered daily at Stockyard Spring.
Camelidae	**Camelus dromedarius* Camel.	**Oct. 1999:** Throughout the survey area. Tracks.
Equidae	**Equus asinus* Donkey.	**Oct. 1999:** Loam 2 and Eil Eil Spring. Old tracks preserved in dried mud.

contrast to the native taxa, the introduced rodent, *M. domesticus,* was abundant on highly saline surfaces, particularly in sites dominated by or close to extensive areas of *S. virginicus.*

Mus domesticus was much less abundant on loamy surfaces and was not detected on red sands. However assemblages of native taxa were considerably more diverse on them than on highly saline ones. Although we recorded approximately equal numbers of species (8 and 7 respectively) on them, and there was some commonality (*e.g.* P. *hermannsburgensis,* P. *nanus* and *M. rufus*), their compositions differed. Thus three taxa (two *Planigale* sp. and *M. agilis*) were only detected on loamy surfaces and three taxa (*S. youngsoni, N. alexis* and *M. lagotis*) on red sands.

Discussion

The only rocky surfaces in the study area are low, calcrete exposures but the area is otherwise geomorphologically and hydrologically diverse and straddles a sharply defined boundary between two bioregions (DL and GSD) of different biological provinces (Torresian and Eremaean). However, diversity of the native mammal fauna was relatively low (*cf.* McKenzie 1981; McKenzie & Youngson 1983), as were population densities in 1999 when five individuals represented four dasyurid species (0.6% trap success in pit traps, dasyurids are not commonly taken in Elliott traps) and 15 individuals represented four native rodent species (0.43% trap success in all traps). Most of those animals were taken in dryer habitats. However, **Mus domesticus* was abundant in saline (*S. virginicus*) grasslands and some adjacent swamps. *E.g.* trap success rates of 12.5% at Fern Spring and (collectively) 8.5% in the two Avicennia sites where others were released without being recorded.

Low numbers may have been a consequence of edaphic conditions. The general condition of the country in 1983 is not known but 88% of the total trap effort for terrestrial species was applied in 1999 (Table 2) when the condition of vegetation indicated there had been no significant rain over the study area for many months and usually-common, arid-zone passerine birds were rare (*e.g.* Singing Honeyeaters, *Lichenostomus virescens,* Black-faced Woodswallows, *Artamus cinereus* and Crimson Chats, *Epthianura tricolor*) although species associated with groundwater-dependent vegetation of mound springs were common (*e.g.* White-plumed Honeyeaters, *Lichenostomus penicillatus*) (Hassell 1999).

For two reasons, it is likely that the recent (post European settlement) mammalian fauna of the area has been, and probably still is, more diverse than shown by

Table 4

Numbers of terrestrial native species (N=12) and **M. domesticus* trapped in each of the three most widespread habitats (Table 1). 'Presence' is noted for taxa that were not trapped. Highly saline habitats were those supporting strongly halophytic vegetation (*Halosarcia* sp., *Sporobolus virginicus* and/or *Avicenna marina*). Fern Spring is treated as highly saline because the vegetation associated with the mound spring occupies a small area within a highly saline landscape and the sampling quadrat incorporated both. Total trap effort was 1845, 885 and 1025 trap nights respectively for saline, loam and sand surfaces.

Family	Taxon	Highly Saline	Other Loams	Red Sands
Dasyuridae	*Planigale maculata*	*	1 (100%)	*
	Planigale spp.	*	1 (100%)	*
	Sminthopsis macroura	3 (100%)	*	*
	Sminthopsis youngsoni	*	*	3 (100%)
Peramelidae	*Macrotis lagotis*	*	*	Present
Macropodidae	*Macropus agilis*	*	Present	*
	Macropus robustus	*	Present	*
	Macropus rufus	Present	Present	Present
Muridae	*Notomys alexis*	*	*	5 (100%)
	Pseudomys desertor	1 (20%)	1 (20%)	3 (60%)
	Pseudomys hermannsburgensis	*	4 (57%)	3 (43%)
	Pseudomys nanus	*	1 (50%)	1 (50%)
	**Mus domesticus*	43 (90%)	5 (10%)	*
Native taxa		3 species	8 species	7 species
Trapped individuals of native taxa		4 animals	13 animals	15 animals

our results. First, some extant species may not have been detected. In particular, the bat fauna may be under represented. Second, many CWR species (Burbidge & McKenzie 1989) have declined throughout much of arid mainland Australia and some are now presumed extinct (*e.g.* McKenzie & Burbidge 2006). The study area is within the former distribution limits of several of them (*e.g.* van Dyck & Strahan 2008; Menkhorst 2001). Nevertheless, two CWR species, *Macrotis lagotis* and *P. nanus* (which, at 35 g, is at the lower end of the CWR; Burbidge & McKenzie 1989) were present and there are recent records of two others from the vicinity. *Lagorchestes conspicillatus,* (Macropodidae) is known from a 2002 record about 90 km northeast of the study area (WA Museum Reg. No. M 54161) and there are two sight records of *Trichosurus vulpecula* (Phalangeridae) on the Great Northern Highway about 50 and 120 km north of the study area respectively (K. Miller, Wildlife Officer, Department of Conservation & Land Management, Broome – pers. comm. to ANS). Habitats similar to those in which both species were recorded occur within the study area and more broadly within the Mandora System.

Table 5 indicates the affinities of all species with Torresian and Eremaean provinces. Representatives of both faunas are present but Eremaean elements predominate. *Macropus agilis,* was the only exclusively (in WA) Torresian species. Three more, a dasyurid, a rodent and a megachiropteran bat are characteristically Torresian but also occur in Eremaean bioregions. In contrast *Planigale* sp., *S. youngsoni* and P. *hermannsburgensis* are more or less exclusively Eremaean. As expected, *S. youngsoni,* and many of the P. *hermannsburgensis* were recorded on red sandy surfaces of the GSD while the Planigale was taken on heavier soil of DL (*cf.* McKenzie & Youngson 1983). Five other species, a dasyurid, a bandicoot, a macropod and two rodents, are characteristically Eremaean but extend into more arid Torresian areas (McKenzie 1981). The remaining species, a macropod, and the three microchiropteran bats are widespread in both provinces.

Besides the admixture of Eremaean and Torresian elements, interesting features of the mammal fauna include the occurrence of the un-named Pilbara *Planigale* so far north, the persistence of small populations of the CWR species *M. lagotis* and *P. nanus* (the most southerly mainland population known to be extant) and the occurrence of *M. agilis.* We are not aware of previously published records of *M. agilis* from so far south but in May 2003, it was reported "in plague numbers" at least 80 km further south-west in coastal (DL) country on Wallal Downs Station (19° 47' S, 120° 39' E; Kingsley Miller personal communication to ANS). Also in May 2003, after heavy overnight rain, many were seen on the side of the Great Northern Highway from the edge of the Mandora paleo-system at 19° 46' S 121° 09' E (near Sandfire Roadhouse) to the edge of Roebuck Plains at 18° 00' S, 122° 36' E (ANS personal observation) and so the species probably occurs continuously in coastal habitats of the Dampierland bioregion from the southwest Kimberley to at least Wallal Downs.

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Table 5

Biogeographic affinities (in WA) of the native mammals recorded in the Mandora study area. *** = essentially endemic, ** = present but not widespread, * = widespread.

Family	Species	Torresian	Eremaean
Dasyuridae	*Planigale maculata*	*	**
	Planigale spp.		***
	Sminthopsis macroura	**	*
	Sminthopsis youngsoni		***
Peramelidae	*Macrotis lagotis*	*	*
Macropodidae	*Macropus agilis*	***	
	Macropus robustus	*	*
	Macropus rufus	**	*
Muridae	*Notomys alexis*	**	*
	Pseudomys desertor	**	*
	Pseudomys hermannsburgensis		***
	Pseudomys nanus	*	**
Pteropodidae	*Pteropus sp.*	*	**
Emballonuridae	*Saccolaimus flaviventris*	*	*
Molossidae	*Chaerephon jobensis*	*	*
Vespertilionidae	*Nyctophilus geoffroyi*	*	*

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Spatial variability in terrestrial fauna surveys; a case study from the goldfields of Western Australia

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Abstract

Although spatial variability in fauna assemblages has been discussed in the literature for many decades, terrestrial fauna surveys undertaken to support environmental impact assessments (EIAs) in Western Australia (WA) rarely adequately address this issue when undertaking surveys of the terrestrial vertebrate ecosystems. The specific objective of this investigation was to describe the spatial variability in the trapped terrestrial vertebrate fauna for five vegetation assemblages in the semi-arid northern goldfields region of WA. The trapped terrestrial vertebrate assemblage differed significantly among replicate sites in both the composition and relative abundance in each of the five habitats. A high proportion of species trapped were singletons and doubletons, and many species demonstrated a patchy distribution within habitats. Both of these parameters provide a strong case for addressing spatial diversity in terrestrial fauna surveys undertaken to support EIAs.

Key words: fauna survey, spatial variability, Western Australia, reptiles, mammals, rarity, environmental impact assessment, EIA

Introduction

The Western Australian (WA) Environmental Protection Authority (EPA) in its Position Statement No 3 Terrestrial Biological Surveys as an Element of Biodiversity Protection (2002) and supporting Guidance Statement No 56, Terrestrial Fauna Surveys for Environmental Impact Assessment in Western Australia (2004) indicated that it requires a proponent of development to undertake appropriate terrestrial fauna surveys to provide sufficient information to address both biodiversity conservation and ecological function values.

To adequately assess potential impacts on ecosystems and ecosystem function, we believe it is necessary that a near complete list of the terrestrial species and their relative abundance is provided for each of the major habitats (see Kodric-Brown & Brown 1993). Although spatial variability and spatial distributions within and among species is an obvious issue that should be addressed in planning terrestrial fauna surveys (see Gaston & Blackburn 2000; Hanski 1999, and references therein), we were unable to find any recent terrestrial fauna surveys undertaken to support EIAs that adequately addressed this issue. If there is high variability in species spatial occupancy, then a single survey site might be inadequate to represent the fauna assemblage in a habitat (Greenwood & Robinson 2006). Greenwood and Robinson (2006) indicated that a single sampling unit can only provide an imprecise estimate for the whole study population, so it is necessary to increase the sampling units to increase precision and representativeness. Typically, terrestrial fauna surveys undertaken for the purpose of preparing an EIA in WA use one or two sampling units in each habitat type (*e.g.* see Bamford Consulting Ecologists 2007; Biota Environmental Sciences 2005a, b, c; Ecologia Environment 2004, 2006; Western Wildlife 2006; Outback Ecology Services 2006).

As a first step in addressing this issue, we set out here to describe the spatial variability in the trapped terrestrial vertebrate fauna in five vegetation assemblages in the semi-arid northern goldfields region of WA. The presence of some rare and conservation significant vertebrate fauna can be assessed as part of a generic terrestrial vertebrate fauna surveys. Other rare and conservation significant species require focussed species-specific searches. This paper only addresses the fauna component of developing an appreciation of the ecological functions of a particular habitat and where generic trapping surveys are expected to identify the presence and abundance of rare and conservation significant species.

An assumption underlying this analysis is that vertebrate fauna assemblages will vary with vegetation assemblages (Thompson *et al.* 2003), which in turn are influenced by physical attributes such as soils, topography and rainfall.

Methods

Study sites

Five distinctly different vegetation assemblages were selected in an area about 30 km south of Wiluna, Western Australia (26° 50'S, 120° 07'E). These were: chenopod shrublands on a flat plain (chenopod); red sand-ridges and swales mostly vegetated with spinifex and low scattered shrubs (sand dune); mulga woodland with an understorey of spinifex (mulga spinifex); mulga woodland without an understorey of spinifex (mulga); and sand plains vegetated with spinifex and scattered shrubs (spinifex sand plain). As the terrestrial fauna assemblage was likely to be different on the sand ridges and adjacent swales, all trapping lines in this habitat were run off the dune onto the swale to ensure trapped fauna would be directly comparable among sites.

The trapping program for each of these five vegetation assemblages was designed to address both temporal and spatial variability in the fauna assemblage and to enable a direct comparison to be made among sites in each vegetation assemblage. For each vegetation assemblage, four 'replicate' sites were selected. The four sites in each vegetation assemblage were far enough apart so as to limit movement of individuals among sites (*i.e.* they were independent, > 500 m apart; Table 1).

Each survey site contained four trap lines. Each trap line contained three 20 L PVC buckets, three 150 mm by 500 mm deep PVC pipes as pit-traps and three pairs of funnel traps evenly spaced along a 30 m fly-wire drift fence that was approximately 250 mm high. In addition, three Elliott traps were set adjacent to each drift fence and one wire cage trap was placed between each pair of drift fences and these traps were baited with rolled oats, peanut butter and sardines.

All pit-traps were dug in during July 2006 to minimise 'digging-in' effects. Digging-in effects occur when particular species are attracted to freshly turned soil in search of prey (*e.g. Varanus gouldi, V. eremius*) and are caught as a result, potentially biasing the catch data. There were two seven day survey periods – 17–23 October 2006, and 11–17 January 2007 to ensure that temporal variation in small vertebrate activity patterns was adequately addressed (see Thompson & Thompson 2005). All traps remained open for a period of seven nights during each survey period. The trapping effort for each of the 20 sites was designed to exceed that which would normally be used by environmental consultants undertaking terrestrial fauna surveys in a vegetation assemblage for the purpose of preparing an EIA (see Biota Environmental Sciences 2005a, b; Ecologia Environmental Consultants 2004, 2006; Western Wildlife 2006; Outback Ecology Services 2006).

All mammals, reptiles and amphibians caught in traps were identified and recorded. Most individuals were released near their point of capture, but away from the traps to minimise immediate recapture. A small number of individuals were vouchered with the Western Australian Museum. Only mammals and reptiles caught are included in this analysis, as the activity pattern of arid-adapted frogs in this area is heavily influenced by patterns of rainfall, and their inclusion in the analysis was likely to distort the results. Incidental observations were not included in the dataset. All captures were marked so that recaptured individuals could be identified. As the rate of recaptures was less than 1% and as most environmental consultants do not record recaptures, all captures were included in the analysis.

Data analysis

Trapped assemblage structure can be measured in numerous ways (Hayek & Buzas 1997; Magurran 2004). The four most common attributes are species richness, evenness, relative abundance and a composite measure of diversity. These metrics are interrelated and there are numerous analytical tools available to quantify differences among assemblages for each of these attributes (Magurran 2004).

Species richness and relative abundance

The actual number of species caught at each site was one measure of species richness and is directly related to the trapping effort and number of individuals caught. Had the trapping effort been extended and more individuals caught it is highly probable that the number of species caught would increase (Colwell & Coddington 1994; Magurran 2004). Colwell and Coddington (1994) reported Chao 2 and Jackknife 2 estimates of species richness provided remarkably accurate estimates for small samples. Chazdon *et al.* (1998) suggested that incidence-based coverage estimator (ICE) and Chao 2 performed well with small samples. Based on these assessments, Chao 2 was used to estimate species richness for each of the sites sampled and was calculated using Colwell's EstimateS software (http://viceroy.eeb.uconn.edu/estimates).

ANOVA (using StatistiXL, V1.6, http: www.statistixl.com) was used to determine significant differences among the number of individuals and the number of species caught in each vegetation assemblage, with the number of individuals and species at each of the four sites in each vegetation assemblage providing the variance. A repeated measures ANOVA was used to test significant difference among the number of individuals caught in each of the nine vertebrate families, with the number of individuals caught at each of the four sites in each vegetation assemblage providing the variance. Sites

Table 1

Location of all trapping sites (UTM Datum WGS 84)

Site #	Chenopod	Sand dunes	Mulga spinifex	Mulga	Spinifex sand plain
1	51 237168E 7025570N	51 243372E 7025229N	51 243063E 7018666N	51 243111E 7016356N	51 241785E 7018871N
2	51 238085E 7025392N	51 23999E1 7027902N	51 243112E 7020014N	51 238889E 7020384N	51 242799E 7017924N
3	51 238454E 7025665N	51 239793E 7027753N	51 243140E 7020828N	51 240503E 7020728N	51 242813E 7017639N
4	51 238672E 7025598N	51 238261E 7029074N	51 243604E 7022375N	51 245212E 7022402N	51 242143E 7018147N

were treated as repeats in this analysis. This was not a powerful analytical tool because the sample sizes for each vegetation assemblage were small. Large differences would therefore be required for a statistical difference to be detected.

Evenness

Magurran (2004) supported Smith and Wilson's (1996) assessment that their measure of evenness (E_{var}) was a satisfactory overall measure. E_{var} was calculated for each of the trapped assemblages using Species, Diversity and Richness software (Pisces Conservation Ltd, V4.0).

Diversity

Log series diversity (Fisher's alpha) was used to measure diversity because of its good discriminating ability and low sensitivity to sample size (Kempton & Taylor 1974; Hayek and Buzas 1997; Magurran 1988). Log series diversity was calculated using Species, Diversity and Richness software (Pisces Conservation Ltd, V4.0). To examine differences in diversity among sampled sites for each vegetation assemblage we adopted Magurran's (2004) advice and compared the slopes of rank/ abundance plots (Whittaker plots). When the relative abundance of each species is log-transformed (Y axis; $\log_{10}$) and plotted against the ranking of species from highest to lowest, the downward sloping line of best fit for undisturbed habitats should approach linearity (Magurran 2004). Presuming these lines are linear, a comparison of the exponents of the regression lines provides a tool for statistically examining differences among diversity for the trapped assemblage for each site in each vegetation assemblage. For our data, we had an unusually high number of singletons in many of the datasets, which reduces the slope of the regression line (and perhaps the assumption of linearity). Singletons can represent individuals that are either rare or vagrants, are difficult to catch using the trapping protocols used or have temporarily moved into a habitat in which they would not normally be found. To address this problem we repeated the comparison of regression line exponents excluding singletons from the dataset, and report the results from both analyses.

Similarity

Our results indicated significant differences among the trapped assemblages between and within vegetation assemblages, so based on this information we wished to indicate the extent to which they were similar. We used the Morisita-Horn index to compare similarity between various combinations of sites and a principle component analysis (PCA) to show affinity among all sites. The quantitative Morisita-Horn similarity index was selected because it is not strongly influenced by either species richness or sample size (Wolda 1981) and was recommended by Magurran (2004); however, it should be noted that it is sensitive to the abundance of the most abundant species. A PCA (using StatistiXL, V1.6, http: www.statistixl.com) was used to provide a multiple dimensional grouping of species.

Results

The local weather conditions for each of the survey periods were typical for October and January for this area. A total of 2783 reptiles and mammals from 61 species were trapped during the October and January surveys (Table 2). There was a significant difference in the number of individuals caught at each of the sites among vegetation assemblages (ANOVA, $F_{4, 15}$ = 4.69, P = 0.012) but no significant difference in the number of species caught (ANOVA, $F_{4, 15}$ = 0.93, P = 0.474). Chao's estimate of species richness varied appreciably among sites for each vegetation assemblage (Table 3). Estimated mean species richness (Chao 2) for at least one site in each vegetation assemblage fell outside the 95% CI range for another site in all vegetation assemblages.

The total number of individuals caught in each of the five vegetation assemblages differed and probably reflected the abundance of small vertebrates in each of the vegetation assemblages. There was also a significant difference in the number of individuals caught in the families at each site (ANOVA, $F_{3,12}$ = 4.0, P = 0.014) and there was no interaction effect among vegetation assemblages ($F_{4,40}$ = 0.372, P = 0.83).

The species accumulation curve for the entire data set indicates that a total of 65 species could be trapped at all sites (*e.g.* the asymptote). In addition to the trapping program that caught 61 species, *Nephrurus milii, Brachyurophis approximans, Parasuta monachus, Pseudechis butleri* and *Suta fasciata* were caught while spotlighting in the five vegetation assemblages but were not caught in traps. All these species have previously been caught in either pit- or funnel traps at other locations.

Of the 61 species caught at all sites, nine were singletons (only caught once) and two were doubletons, indicating that there was a high proportion (14.8% and 3.3% respectively; Table 3) of species that were rarely caught in traps and would reduce similarity scores calculated to compare vertebrate fauna assemblages among vegetation assemblages (Table 4). Because sample sizes were appreciably smaller for sites than the combine sites for each vegetation assemblage, there were many more singletons and doubletons in the site catch data.

The shape of species accumulation curves for individual sites differed within vegetation assemblages. Thompson and Withers (2003) explained how the shape of the species accumulation curve could be used to understand the assemblage structure, as it is influenced by both relative abundance and species richness. Sites with a high proportion of rare species and a few abundant species have a species accumulation curve with a low 'shoulder' (inflection point on the ordinate axis) and a long upward slope to the asymptote, whereas sites with a high proportion of relatively abundant species have a steeply rising initial slope to the species accumulation curve and plateaux early. An inspection of the species accumulation curves in Figure 1 indicates appreciable difference among sites for each vegetation assemblage in vertebrate assemblage structure.

Fisher's alpha diversity score for the combined data for all 20 sites was 11.03. As expected, diversity was lower in each of the 20 survey sites (Table 3) with the mulga spinifex habitat type having the lowest variability in diversity, as measured by the standard deviation (0.76) for its four sites, followed by the spinifex sand plain habitat (0.79), the sand dune habitat (1.31), the mulga

Table 2

Vertebrates trapped during the October 2006 and January 2007 in 20 sites, four of which were in each of five vegetation assemblages.

Species	Sand Dune					Mulga					Mulga Spinifex					Chenopod					Spinifex Sand Plain					Total all sites
	Site 1	Site 2	Site 3	Site 4	Total	Site 1	Site 2	Site 3	Site 4	Total	Site 1	Site 2	Site 3	Site 4	Total	Site 1	Site 2	Site 3	Site 4	Total	Site 1	Site 2	Site 3	Site 4	Total	
Mammals																										
Dasyuridae																										
Antechinomys laniger																								1	1	1
Dasycercus cristicauda																					4	2	1		7	7
Ningaui ridei	4	4	3	14	25			2		2	13	4	15		32		2			2	16	11	21	26	74	135
Sminthopsis macroura	1				1	3	6			9							3	1	1	5						15
Sminthopsis hirtipes			1		1																					1
Sminthopsis ooldea	2	2	2	2	8	11	2	1	5	19	2	4	11	3	20		5	3	4	12	1		2	3	6	65
Muridae																										
Mus musculus	3	3	4	14	24	1				1		1	1		2	5	2	4	5	16		1	1	3	5	48
Notomys alexis	20	39	13	39	111	13	15	26	29	83	26	23	14	7	70	4	10	5	17	36	5	17	19	10	51	351
Pseudomys desertor	1	3	1	5	10	2	2	2	3	9	5	4	3	1	13	4	3	1	6	14	10	3	2	3	18	64
Pseudomys hermannsburgensis	12	5	5	13	35	9	2	12	5	28	5	1	13	5	24	8	7	9	12	36	2	9	20	8	39	162
Reptiles																										
Gekkonidae																										
Diplodactylus conspicillatus			5		5	8	4	9	9	30	8			21	29	4				4	1	3	29	10	43	111
Diplodactylus pulcher						1	5		1	7						1				1						8
Gehyra variegata	2	1	6		9		1		1	2	4		1		5		1		1	2		1		1	2	20
Heteronotia binoei																							1		1	1
Lucasium squarrosum							10	2	2	14							1			1						15
Nephrurus laevissimus	37	14	28	15	94																					94
Nephrurus vertebralis	2	1		1	4			1	2	3			1		1			1	2	3						11
Rhynchoedura ornata	1	3	15	1	20	8		7	14	29		5			5	12	13	32	26	83			8	2	10	147
Strophurus elderi				8	8			2	1	3	9	1	9		19						16	22	8	18	64	94
Strophurus strophurus				1	1													2	1	3						4
Strophurus wellingtonae						7		1	3	11		1	2	1	4											15
Pygopodidae																										
Aprasia picturata													1		1											1
Delma butleri	1			6	7							1			1						4			2	6	14
Delma nasuta				3	3									1	1		1			1	1				1	6
Lialis burtonis		1		4	5						2				2		3		1	4		1	1	1	3	14
Pygopus nigriceps	1				1		2	2		4	1	1	1	2	5			2	1	3						13
Scincidae																										
Ctenotus ariadnae											7	7	7	7	28	1				1	14	10	7	13	44	73
Ctenotus grandis											10		7	1	18						5	10	2	8	25	43
Ctenotus helenae	2	3	8	26	39	2		17	2	21	32	11	56	12	111	14	3		1	18	18	29	17	53	117	306
Ctenotus leonhardii	8	2	13	7	30	20		25	14	59	19	47	20	25	111	32	20	21	14	87		3	17	6	26	313
Ctenotus pantherinus						3		5	1	9	47	2	54	20	123						19	39	30	72	160	292
Ctenotus schomburgkii						7	2	6	7	22		1			1	3			1	4						27

Egernia depressa		1			1	3			1	4																5
Egernia inornata												8			8	6				6				1	1	15
Eremiascincus richardsonii																			1	1						1
Lerista desertorum	2			1	3			1		1		10	7	2	19	2		4	1	7	1				1	31
Lerista rhodonoides									1	1			1		1											2
Menetia greyii		2	1		3		2		2	4	3	4	4	4	15	6	2	2	3	13		1	1		2	37
Tiliqua multifasciata											1				1						3				3	4
Agamidae																										
Caimanops amphiboluroides						1	1			2																2
Ctenophorus isolepis	6		1		7				2	2	9	4		1	14						8	6	15	9	38	61
Ctenophorus nuchalis	4		1		5												16	1		17				1	1	23
Ctenophorus reticulatus							1		2	3																3
Ctenophorus salinarum	1				1																					1
Ctenophorus scutulatus				2	2		1	1	12	14																16
Lophagnathus longirostris			1		1																					1
Moloch horridus		1			1																					1
Pogona minor	1				1									1	1			1	1	2	1		1	1	3	7
Varanidae																										
Varanus brevicauda			1		1								1	1	2						3	5	1	6	15	18
Varanus caudolineatus						1	2	1	1	5							1			1						6
Varanus eremius											2				2						1	1	4	1	7	9
Varanus gouldii	1	1			2				1	1		2	1		3											6
Varanus panoptes	3	1	2	4	10		1		1	2	2		1	1	4	2		3	1	6		1			1	23
Varanus tristis								1		1																1
Elapidae																										
Brachyurophis semifasciata	1				1			1		1	1				1			3		3				2	2	8
Furina ornata	2			1	3																		1		1	4
Pseudonaja modesta								2	1	3													1		1	4
Pseudonaja nuchalis			1	2	3	1				1								2	1	3						7
Simoselaps bertholdi		1			1													2	2	4			1		1	6
Typhlopidae																										
Ramphotyphlops hamatus	1				1							1		1	2				4	4						7
Ramphotphylops waitii				1	1									1	1		1			1						3
Grand Total	119	88	112	170	489	101	59	127	123	410	208	143	231	118	700	104	94	99	107	404	133	175	211	261	780	2783
Total # Species	25	19	20	22	40	18	17	22	26	35	21	22	23	21	37	15	18	19	23	34	20	20	25	25	35	61
# Mammal species	7	6	7	6		6	5	5	4		5	6	6	4		4	7	6	6		6	6	7	7		10
# Reptile species	18	13	13	16		12	12	17	22		16	16	17	17		11	11	13	17		14	14	18	18		51
# Dasyuridae	5	4	3	14		3	6	2	0		13	4	15	0		0	5	1	1		20	13	22	27		158
# Muridae	38	52	26	73		36	21	41	42		38	33	42	16		21	27	22	44		18	30	44	27		691
# Gekkonidae	42	19	54	26		24	20	22	33		21	7	13	22		17	15	35	30		17	26	46	31		520
# Pygopodidae	2	1	0	13		0	2	2	0		3	2	2	3		0	4	2	2		5	1	1	3		48
# Scincidae	12	8	22	34		35	4	54	28		119	90	156	71		64	25	27	21		60	92	74	153		1149
# Agamidae	12	1	3	2		1	3	1	16		9	4	0	2		0	16	2	1		9	6	16	11		115
# Varanidae	4	2	3	4		1	3	2	3		4	2	3	2		2	1	3	1		4	7	5	7		63
# Elapidae	3	1	1	3		1	0	3	1		1	0	0	0		0	0	7	3		0	0	3	2		29
# Typhlopidae	1	0	0	1		0	0	0	0		0	1	0	2		0	1	0	4		0	0	0	0		10
Fisher's Alpha	9.65	7.45	7.09	6.73		6.37	8.00	7.68	10.07		5.82	7.26	6.35	7.43		4.81	6.61	6.99	9.00		6.53	5.82	7.38	6.80		11.03

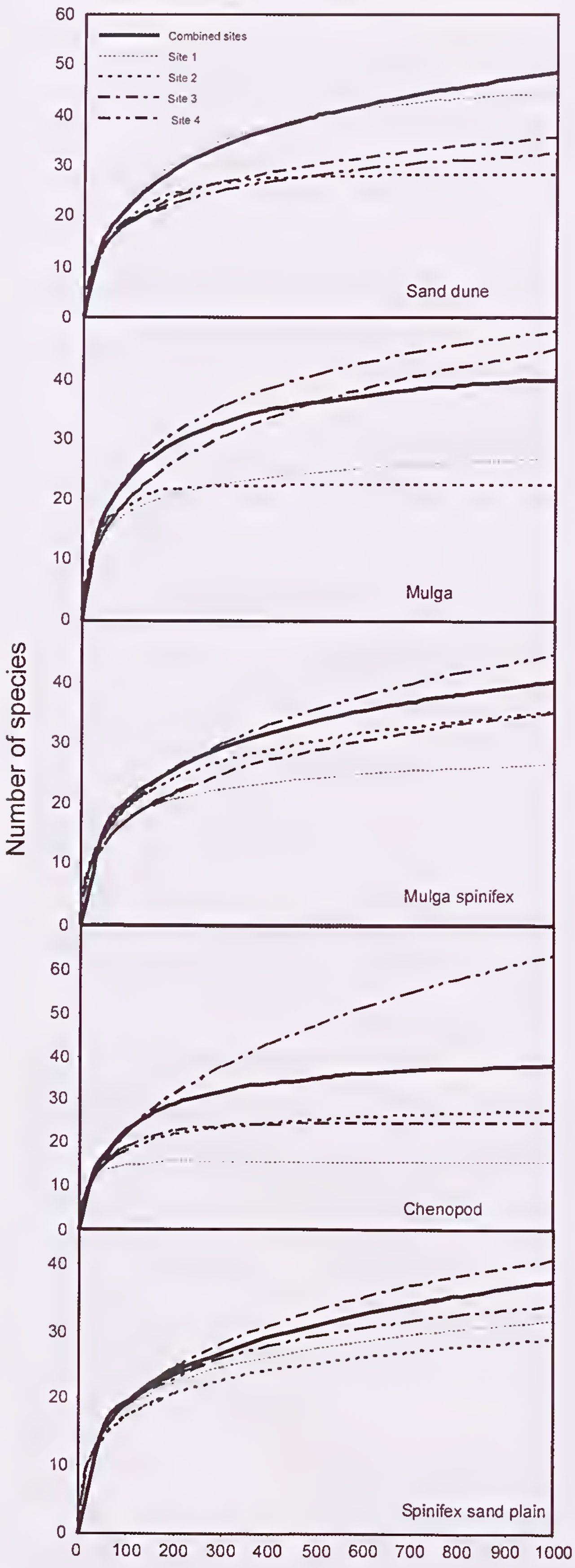

Figure 1. Species accumulation curves for each site and the combined sites for each vegetation assemblage.

habitat (1.53) and with the highest being the chenopod habitat (1.72). Alpha diversity scores varied among sites for each vegetation assemblage (Table 3).

The slope of regression lines for the Whittaker plots differed significantly for the sand dune ($F_{3,75}$ = 4.51, P < 0.01), mulga ($F_{3,75}$ = 4.72, P < 0.01) and the spinifex sand plain ($F_{3,81}$ = 3.04, P < 0.01) habitats, but did not differ for the chenopod ($F_{3,67}$ = 2.41, P = 0.07) and mulga spinifex ($F_{3,79}$ = 1.02, P = 0.39) sites. However, when singletons were removed, only the slopes for the sites in the mulga spinifex habitat ($F_{3,49}$ = 4.76, P < 0.01) differed significantly [chenopod ($F_{3,43}$ = 1.58, P = 0.21), sand dune ($F_{3,46}$ = 0.86, P = 0.47), mulga ($F_{3,47}$ = 1.70, P = 0.18) and spinifex sand plain ($F_{3,53}$ = 1.16, P = 0.33)]. This difference in the regression line slopes with and without singletons in the data sets indicates the appreciable influence that singletons were having on the assemblage structure. Therefore it was anticipated that evenness values would differ among sites in each vegetation assemblage (Table 3) and for each vegetation assemblage at least one mean value fell outside the 95% confidence limits for another site in that vegetation assemblage.

The proportion of shared species among the five different vegetation assemblages varied from 54 to 80% (Table 4). The most dissimilar fauna assemblages measured using the Morisita-Horn similarity index were the chenopod and the spinifex sand plain habitats (0.28), and the most similar were the mulga spinifex and spinifex sand plain (0.87). The mean Morisita-Horn similarity score among fauna assemblages (0.56) for the five vegetation assemblages was lower than for each of the sites for each vegetation assemblage (0.76 for chenopod, 0.71 for sand dune, 0.68 for mulga spinifex, 0.89 for mulga and 0.81 for spinifex sand plain). Variability in the Morisita-Horn scores among sites for each vegetation assemblage, as measured by the standard deviation, was lowest for the chenopod habitat (0.072), followed by the spinifex sand plain habitat (0.093), the sand dune habitat (0.097), the mulga habitat (0.158) and highest among the mulga spinifex sites (0.165).

Eigenvalues for PCA 1 and 2 were 10.4 and 7.2 respectively, and accounted for 17.0 and 11.9% of total variance. The PCA separated the mulga spinifex, spinifex sand plain and mulga habitats on the first PCA (Figure 2), but there was overlap between the mulga and mulga spinifex with chenopod and sand dune sites. The sand dune and chenopod habitats were separated from the other three vegetation assemblages on PCA 2, but there was an overlap between the fauna assemblages in each of these vegetation assemblages. Only the spinifex sand plain sites clustered closely, there was an obvious 'outlier' for the mulga and sand dune sites, and some distance between fauna assemblages in the chenopod and mulga spinifex habitats. The fauna assemblage at one mulga spinifex habitat was closer to the spinifex sand plain sites, and the fauna assemblage at one mulga site was closer to that in a mulga spinifex assemblage than other sites within its vegetation assemblage.

Table 3

Chao 2 estimate of species richness, alpha diversity scores, and the number of singletons and doubletons for all sites and vegetation assemblages

Habitat type	Site	Trapped species richness	Species richness – Chao 2 (lower and upper 95% CI)	Alpha diversity	Evenness – E_{var} (lower and upper 95% CI)	Singletons (n/%)	Doubletons (n/%)
Mulga	All sites	35	38.25 (35.66 – 52.75)	9.16	0.35 (0.32 – 0.46)	7 (20.0)	5 (14.3)
	Site 1	18	20.32 (18.34 – 33.96)	6.37	0.50 (0.45 – 0.67)	5 (27.8)	2 (11.1)
	Site 2	17	18.16 (17.15 – 26.01)	8.00	0.63 (0.50 – 0.73)	5 (29.4)	7 (41.2)
	Site 3	22	25.57 (23.22 – 47.39)	7.68	0.43 (0.38 – 0.58)	8 (36.4)	6 (27.3)
	Site 4	26	31.39 (27.39 – 51.59)	10.07	0.49 (0.42 – 0.58)	10 (38.5)	6 (23.1)
Mulga spinifex	All sites	37	47.21 (39.53 – 78.19)	8.34	0.25 (0.24 – 0.33)	9 (24.3)	4 (10.8)
	Site 1	21	22.11(21.13 – 30.79)	5.82	0.42 (0.36 – 0.54)	3 (14.3)	4 (19.1)
	Site 2	22	30.67 (23.79 – 63.98)	7.26	0.43 (0.39 – 0.56)	8 (36.4)	2 (9.1)
	Site 3	23	34.14 (25.46 – 73.56)	6.35	0.32 (0.03 – 0.45)	9 (39.1)	1 (4.4)
	Site 4	21	34.93 (24.24 – 80.88)	7.43	0.41 (0.37 – 0.53)	10 (47.6)	2 (9.5)
Chenopod	All sites	34	38.88 (34.92 – 59.85)	8.86	0.36 ((0.32 – 0.45)	7 (20.6)	2 (5.9)
	Site 1	15	15.31 (15.02 – 20.64)	4.81	0.55 (0.44 – 0.70)	2 (13.3)	2 (13.3)
	Site 2	18	19.55 (18.21 – 29.30)	6.61	0.51 (0.43 – 0.65)	5 (27.8)	3 (16.7)
	Site 3	19	21.32 (19.37 – 33.38)	6.99	0.52 (0.41 – 0.60)	5 (26.3)	5 (26.3)
	Site 4	23	59.21 (32.35 – 163.24)	9.00	0.46 (0.40 – 0.62)	12 (52.2)	2 (8.7)
Sand dune	All sites	40	68.17 (44.65 – 144.65)	10.32	0.31 ((o,29 – 0.39)	14 (35.0)	2 (5.0)
	Site 1	25	31.38 (26.57 – 50.09)	9.65	0.50 (0.41 – 0.57)	10 (40.0)	6 (24.0)
	Site 2	19	24.20 (20.06 – 44.42)	7.45	0.52 (0.42 – 0.59)	8 (42.1)	3 (15.8)
	Site 3	20	28.67 (21.79 – 61.98)	7.09	0.44 (0.41 – 0.59)	8 (40.0)	2 (10.0)
	Site 4	22	28.50 (23.24 – 56.140	6.73	0.41 (0.37 – 0.56)	6 (27.3)	3 (13.6)
Spinifex sand plain	All sites	35	43.36 (36.97 – 70.54)	7.54	0.23 (0.22 – 0.31)	10 (28.6)	3 (8.6)
	Site 1	20	23.48 (20.59 – 40.65)	6.53	0.45 (0.45 – 0.62)	6 (30.0)	1 (5.0)
	Site 2	20	26.96 (21.22 – 59.70)	5.82	0.38 (0.34 – 0.53)	6 (30.0)	1 (5.0)
	Site 3	25	35.45 (27.45 – 69.55)	7.38	0.33 (0.32 – 0.45)	10 (40.0)	3 (12.0)
	Site 4	25	28.90 (25.73 – 45.95)	6.80	0.35 (0.32 – 0.45)	7 (28.0)	3 (12.0)
All sites				11.03		9 (14.8)	2 (3.3)

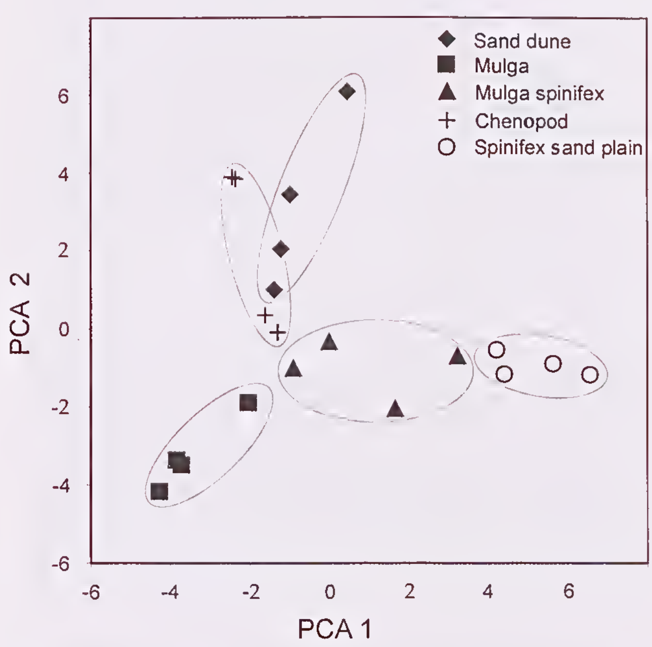

Figure 2. PCA 1 and 2 of the trapped fauna assemblage for all 20 survey sites.

Discussion

Habitat generalists and specialists

Trapped fauna assemblages differed among sites for each vegetation assemblage. Within any fauna assemblage, species sit on a continuum from those that are habitat generalists to those that are habitat specialists. Habitat generalists are those species that are quite plastic in their habitat requirements and are found in a diverse range of habitat types, whereas habitat specialists have specific habitat requirements, often with limited tolerances. Pianka (1969; 1972) and Pianka & Pianka (1976) were one of the first to categorise Australian arid and semi-arid reptiles into habitat generalists and specialists. For example, Pianka (1969) categorised arid and semi-arid Western Australian reptile species into four groups based on habitat preferences: ubiquitous, spinifex, mulga and sand ridges. It was therefore expected that some species would be common across all five vegetation assemblages and others would be restricted to one or two vegetation assemblages. In addition, some species can be evenly distributed over a large section of suitable habitat, with minor variation in relative abundance from one site to the next, whereas the distribution of other species can be very patchy, with relatively high densities in some areas and being absent in many others, although the entire area offers suitable habitat (Hanski 1999). Hanski (1999) suggested that species that are locally abundant, occur in relatively

Table 4

Similarity scores for captured fauna assemblages among vegetation assemblages and among survey sites in each habitat type (numbers in parenthesis are the recorded species richness for that habitat type)

		Shared species observed	Morisita-Horn Similarity Index
Mulga (35)	Mulga spinifex (37)	24	0.66
	Chenopod (34)	23	0.75
	Sand dune (40)	24	0.69
	Spinifex sand plain (35)	19	0.43
Mulga spinifex (37)	Chenopod (34)	25	0.54
	Sand dune (40)	27	0.49
	Spinifex sand plain (35)	28	0.87
Chenopod (34)	Sand dune (40)	27	0.50
	Spinifex sand plain (35)	22	0.28
Sand dune (40)	Spinifex sand plain (35)	25	0.39
Mulga			
Site 1 (18)	Site 2 (17)	10	0.46
	Site 3 (22)	12	0.83
	Site 4 (26)	14	0.80
Site 2 (17)	Site 3 (22)	10	0.54
	Site 4 (26)	14	0.67
Site 3 (22)	Site 4 (26)	17	0.82
Mulga spinifex			
Site 1 (21)	Site 2 (22)	13	0.53
	Site 3 (23)	15	0.92
	Site 4 (21)	14	0.77
Site 2 (22)	Site 3 (23)	16	0.46
	Site 4 (21)	14	0.68
Site 3 (23)	Site 4 (21)	15	0.70
Chenopod			
Site 1 (15)	Site 2 (18)	8	0.74
	Site 3 (19)	9	0.74
	Site 4 (23)	11	0.67
Site 2 (18)	Site 3 (19)	10	0.75
	Site 4 (23)	12	0.76
Site 3 (19)	Site 4 (23)	17	0.89
Sand dune			
Site 1 (25)	Site 2 (19)	14	0.71
	Site 3 (20)	14	0.86
	Site 4 (22)	15	0.66
Site 2 (19)	Site 3 (20)	13	0.60
	Site 4 (22)	13	0.78
Site 3 (20)	Site 4 (22)	12	0.64
Spinifex sand plain			
Site 1 (20)	Site 2 (20)	14	0.88
	Site 3 (25)	16	0.69
	Site 4 (25)	16	0.84
Site 2 (20)	Site 3 (25)	18	0.76
	Site 4 (25)	17	0.94
Site 3 (25)	Site 4 (25)	19	0.75

unfragmented habitats and are predisposed to high mobility will have few empty areas in suitable habitat. In contrast, species with low densities, occupying highly fragmented habitats and with a low predisposition to migration will have lots of empty areas in suitable habitat. These latter species can also have a wide geographic distribution but are scarce everywhere (*e.g. Antechinomys laniger*). It is these latter species that are likely to be missed in surveys that catch few individuals or are undertaken at a few sites. These species are described as scarce and patchy.

For the five vegetation assemblages surveyed south of Wiluna, there were some species that were obviously restricted to a particular vegetation assemblage (*i.e.* specialist; *e.g. Dasycercus cristicauda, Nephrurus laevissimus*) and there were others that were found in all vegetation assemblages (*i.e.* generalists) and at all sites (*e.g. Notomys alexis, Pseudomys desertor, Pseudomys hermannsburgensis*). There are species that were also found in each vegetation assemblage, but not in each site in each vegetation assemblage (Table 2), or their abundance varied appreciably among replicate sites. These are the species with patchy distributions, and who maybe locally abundant but go undetected in single site surveys for a vegetation assemblage.

Variability among replicate sites

If vegetation assemblages were homogenous and species were evenly dispersed across these habitats, then it probably would not matter where in each vegetation assemblage the sampling was undertaken and only one survey unit would be sufficient to detect all the species present presuming sufficient trapping effort was applied. However, in this survey the total number of shared species recorded among sites for each vegetation assemblage ranged from 47–75% (Table 4), indicating that species were not evenly distributed in each vegetation assemblage. These are species whose distributions are described earlier as patchy.

It is apparent from Tables 2, 3 and 4 that not only was there a significant difference in relative abundance of small vertebrates among vegetation assemblages, there were appreciable differences in measures of evenness and diversity among sites within vegetation assemblages. There were also significant differences among the number of individuals caught in each of the vertebrate families (see Table 2) among sites in each vegetation assemblage. Further, there was an appreciable difference in the number of individuals caught for some species among sites within a vegetation assemblage. For example, an extreme case of this was the number of *Ctenotus pantherinus* caught at the four mulga spinifex habitat sites and the number of *Ctenotus leonhardii* caught at all sites. This variability in the relative abundance of species is reflected in the low similarity scores among sites for each vegetation assemblage (Table 4).

It was anticipated that the surveyed sites would cluster within groups related to the vegetation assemblage to which they belong in the PCA. This is the case for the sites in the spinifex sand plain habitat and less so for the sites in the mulga and mulga spinifex vegetation assemblages. There was an obvious overlap in vertebrate fauna assemblages for the sand dune and chenopod vegetation assemblages, and a close affinity between one of the mulga spinifex and spinifex sand plain sites and a mulga site with a mulga spinifex site. For some vegetations assemblages, if only one site was surveyed, then the data could have appreciably misrepresented the fauna assemblage for the rest of that habitat.

Rare, range restricted and conservation significant species

Often of the focus of terrestrial fauna surveys undertaken to support EIAs is to identify the presence of rare, range restricted or conservation significant species. Rare is generally defined in terms of low abundance or small geographical range (Gaston 1997). Those with a small geographic range can be further subdivided into extent of occurrence, or the distance or area between the outer most limits of its occurrence, with the area of occupancy being the sites within its geographical range in which it is found (Gaston & Blackburn 2000). Some rare species can be abundant in areas that they occupy, but these are low in number or small in size. In addition, species can be deemed rare when they are difficult to trap, but are locally abundant. High levels of trapping are more likely to catch species that are both low in abundance and difficult to catch. Because of the trapping intensity in this survey, it is likely that we were catching species that were both low in abundance and difficult to catch (*e.g. A. laniger, D. cristicauda, S. hirtipes, A. picturata*). But because these species were caught in low numbers they contribute to appreciable differences in the fauna assemblage caught at each site in different vegetation assemblages. Our data indicate the need to collect large and multiple samples in each vegetation assemblage in order to record species that are rare or patchy in their abundance.

Trapping effort

In this survey the total number of trapped vertebrates in each vegetation assemblage generally exceeded the number of individuals caught by environmental consultants when undertaking fauna surveys to prepare EIAs (see Bamford Consulting Ecologists 2007; Biota Environmental Sciences 2005a, b; Ecologia Environmental Consultants 2004, 2006; Western Wildlife 2006; Outback Ecology Services 2006), yet the proportion of singletons caught in each vegetation assemblage was high (Table 3) and four of the five species accumulation curves for the combined data did not plateau indicating that only in the chenopod habitat were 90% of the species caught, suggesting that many of these other surveys would have failed to record numerous species. The EPA (2002) requires proponents of a development to ensure its biological surveys provide sufficient information to address both biodiversity conservation and ecological function values. We suggest that knowledge of both species richness and relative abundance are necessary to understand ecological function values of a habitat. To achieve this, an adequate number of individuals should be caught in each vegetation assemblage and sufficient replicate survey sites should be sampled. To detect the presence of species that have a low abundance over a large geographical distribution, large samples would be the preferred sampling protocol. To detect the presence of species that are locally abundant but have few areas of occupancy within their preferred habitat, then increasing the number of sampling sites would be the preferred protocol.

For a defined trapping effort (limited by time or resources), we have insufficient data to indicate whether it is better to increase the number of individuals caught at a few sites, or to increase the number of sampling sites but catch a lower number of individuals per site to increase the precision for the sample to represent the population. Read *et al.* (1988) compared trap sampling success for small mammals when traps were set out in a grid and along a line transect, and concluded that capture data were highly sensitive to sampling intensity when traps were set in a grid formation and were unlikely to represent true community diversity. However, this sensitivity in the grid formation varied appreciably based on trapping intensity. In contrast, capture data from traps set along a line transect were less influenced by intensity difference and provided a more accurate representation of true community diversity. Read *et al.* (1988) did not assess the protocol of multiple grids spread throughout a vegetation community, which may capture the benefits of both strategies.

In our study, all grids were uniformly spaced within each trapping site, with trap lines being approximately 20 m apart. It would therefore be interesting to compare capture data for mammals and reptiles from an equal number of traps set in a series of grids (*e.g.* 48 traps x 4 sites) with that in a linear transect (192 traps) through a uniform vegetation assemblage.

Conclusions

This investigation has demonstrated appreciable differences in both the composition and relative abundance in the trapped terrestrial vertebrate assemblage among replicate survey sites in each of five vegetation assemblages. Even when trapping yielded many more individuals than would normally be captured by environmental consultants in a vegetation assemblage, there was a high proportion of species that were singletons and doubletons and many species demonstrated a patchy distribution. These data support the Thompson *et al.* (2007) argument for trapping a much larger number of individuals in each vegetation assemblage than is the current practice and Greenwood and Robinson's (2006) argument for using multiple replicates in order to improve precision and representativeness in fauna surveys undertaken to prepare EIAs.

The WA Environmental Protection Authority's (2004) Guidance Statement No 56, *Terrestrial Fauna Surveys for Environmental Impact Assessment in Western Australia* does not address the issue of spatial variability in fauna assemblages and therefore provides no guidance on how terrestrial fauna surveys should be designed to accommodate this issue. This omission needs to be addressed, given that this is the document that environmental consultants use in designing surveys for the purposes of preparing EIAs.

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Distribution and spread of the introduced One-spot Livebearer *Phalloceros caudimaculatus* (Pisces: Poeciliidae) in southwestern Australia

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Abstract

The One-spot Livebearer, *Phalloceros caudimaculatus*, is a neotropical poeciliid maintained as an ornamental fish by hobbyists worldwide. Introduced populations occur in Africa, New Zealand and Australia. This species has been recorded in four Australian states/territories and is now widely dispersed within metropolitan Perth (Swan/Canning catchment) in southwestern Australia. *Phalloceros caudimaculatus* thrives in urban, aquatic habitats (*e.g.* degraded creeks and storm-water drains) and its range in southwestern Australia is expanding into larger watercourses as a consequence of natural dispersal and human-mediated translocations. *Phalloceros caudimaculatus* has dominated habitats in southwestern and eastern Australia that previously contained high densities of *Gambusia holbrooki*, a highly invasive species with documented impacts on aquatic ecosystems and endemic ichthyofauna. This is of concern as little research has been conducted on the potential ecological impacts of *P. caudimaculatus* in Australia or worldwide. As *P. caudimaculatus* is not commonly kept as an ornamental fish in Australia, the inherent risk of release is lower than that of other popular ornamental fishes. However, the recent establishment of a population in New South Wales indicates that the release of fish, and subsequent colonisation of suitable environments, could occur in other areas of Australia.

Keywords: Australia, Caudo, ecosystem disturbance, freshwater fish, *Gambusia holbrooki*, human-assisted dispersal, introduced species, One-spot Livebearer, *Phalloceros caudimaculatus*, translocation

Introduction

The last three or four decades have seen the establishment of numerous populations of introduced, ornamental fishes in Australia (Arthington & McKenzie 1997; Allen *et al.* 2002). Deliberate, human-mediated translocation is the major vector (Arthington & Mackenzie 1997; Lintermans 2004) with primarily cichlids and poeciliids establishing self-maintaining populations. Many poeciliids are adaptable and tolerant of variable environmental conditions and will thrive in modified and degraded aquatic habitats (Meffe & Snelson 1989). Habitat degradation, including pollution, urban land uses, loss of riparian vegetation and altered hydrological regimes, may disadvantage indigenous species while aiding the establishment of adaptable, introduced fishes (Arthington *et al.* 1990; Moyle & Light 1996).

The One-spot Livebearer or Caudo, *Phalloceros caudimaculatus* (Fig. 1), is a small poeciliid native to fresh/estuarine waters of the central-eastern seaboard of South America, from Brazil (approximately Rio de Janiero southwards), Argentina, Uruguay and Paraguay (Rosen & Bailey 1963; Almirón *et al.* 2000; López *et al.* 2005). Although one of the first poeciliids maintained by hobbyists (Innes 1946; Kempkes & Schäfer 1998), it is not as popular as other species from this family (*e.g.* Swordtail *Xiphophorus helleri*, and Guppy *Poecilia reticulata*) due to its drab coloration (McDowall 1999). Like many poeciliids, *P. caudimaculatus* is sexually dimorphic with females and males attaining lengths of 60 and 35mm respectively (Trendall & Johnson 1981). Unlike many tropical ornamental fishes, *P. caudimaculatus* is cold tolerant (Hoedman 1974; Merrick & Schmida 1984; Maddern 2003), surviving temperatures as low as 5°C. While indigenous South American populations inhabit shallow, vegetated stream margins with low water flow (*e.g.* Castro & Casatti 1997; Aranha *et al.* 1998; Almirón *et al.* 2000; Eichbaum-Esteves & Lobon 2001; Machado *et al.* 2002; Casatti 2004; Casatti 2005), *P. caudimaculatus* is also known to occupy highly-modified habitats (*i.e.* streams affected by loss of riparian vegetation and by silt), and estuarine lagoons within its native range (*e.g.* Penczak *et al.* 1994; Araújo 1998; Garcia *et al.* 2003; Casatti 2004; Lima-Junior *et al.* 2006).

Worldwide, *P. caudimaculatus* is not common as an introduced species and has, at present, only become well established in southwestern Australia. It was introduced to Malawi in Africa (Jubb 1977; Welcomme 1981) and is restricted to the Nswadzi River, a small tributary of the Ruo River. It has not spread into the latter river system

Figure 1. Female *Phalloceros caudimaculatus* (45 mm total length) collected from Lesmurdie Brook in southwestern Australia.

since release in the early 1950s (Denis Tweddle, J.L.B. Smith Institute of Ichthyology, pers. comm.). In New Zealand, this species was recorded in several livestock water troughs near Kamo, in Northland (McDowall 1999), although the current status of this population remains unclear (McDowall 2004). Within Australia, *P. caudimaculatus* has been recorded in four Australian states/territories. Its presence has been noted in outdoor ponds in South Australia (Arthington & Lloyd 1989), and in the Todd River Drainage near Alice Springs, Northern Territory (Unmack 2001). Similarly, the present status of these populations is unknown. In 2002, *P. caudimaculatus* was collected from a series of ponds in Long Reef Golf Course in New South Wales near Sydney (Rowley *et al.* 2005), and despite attempts to eradicate this population using rotenone, it thrives at the latter locality (Rayner & Creese 2006). After the discovery of this population in NSW, *P. caudimaculatus* was immediately listed as a noxious species under the NSW Fisheries Management Act.

This paper documents the historical distribution and range expansion of *P. caudimaculatus* in southwestern Australia. The likelihood of further range expansions through natural dispersal and human-mediated translocations in southwestern Australia, and wider Australia, are also discussed. The further spread of *P. caudimaculatus* is of concern as the species has dominated two urban creeks in southwestern Australia (Maddern 2003), and ornamental ponds in Sydney (Rowley *et al.* 2005), that previously contained large populations of the highly-invasive fish, *Gambusia holbrooki*. *Gambusia holbrooki* is the most abundant introduced poeciliid in Australia (Lintermans 2004) due to wide release as a mosquito biological control agent and it is considered a pest because of deleterious impacts on indigenous fishes and ecosystems (McKay 1978; Merrick & Schmida 1984; Arthington 1991; Gill *et al.* 1999; Allen *et al.* 2002; Morgan *et al.* 2004). At this time it is unknown if *P. caudimaculatus* could have similar impacts. Thus, baseline distribution data are important for determining future range expansions and potential ecological impacts of *P. caudimaculatus*, particularly as such data are often lacking for invasive freshwater fishes in Australia (Koehn & Mackenzie 2004).

Materials and methods

The Western Australian capital, Perth, is located within the Swan/Canning catchment (Fig. 2) which is part of the Southwest Drainage Division of Western Australia. This region has a Mediterranean climate with moderate precipitation, principally during winter (Astill & Lavery 2004). The Swan/Avon River to the east, and the Canning River (which confluences with the Southern/ Wungong River) to the south, have catchments of c. 119 000 km^2 and 20 000 km^2, respectively (Thurlow *et al.* 1986). Many watercourses in the Swan/Canning system are contained within the Perth metropolitan area, and are therefore anthropogenically modified to varying degrees (Hodgkin 1987; Swan River Trust 2002). Modifications to aquatic habitats may include altered hydrological regimes, presence of non-indigenous vegetation, sedimentation and pollution (nutrient enrichment and solid refuse) (Storey *et al.* 2000; Swan River Trust 2002).

Qualitative sampling by electrofishing (Fig. 3) was undertaken in metropolitan Perth (31°51'–32°14'S, 115°46'– 116°13'E) between 2002 and 2006. During sampling, endemic ichthyofauna were recorded and returned whilst *P. caudimaculatus* and *G. holbrooki* were retained if captured. For a greater description of some sample sites within this region see Storey *et al.* (2000) and Maddern (2003). Voucher specimens of *P. caudimaculatus* are lodged with the Western Australian Museum and specimen photographs were submitted to the FISHBASE online database (http://www.fishbase.org).

Results and Discussion

Distribution in southwestern Australia

The presence of *P. caudimaculatus* in WA, at two locations in metropolitan Perth (Fig. 2), was noted in published literature almost four decades ago. Griffiths (1972) collected *P. caudimaculatus* (erroneously identified as *Gambusia affinis holbrooki*) at South Perth, with specimens from this location subsequently correctly identified by Trendall & Johnson (1981). This population was observed in an open drain running into ornamental

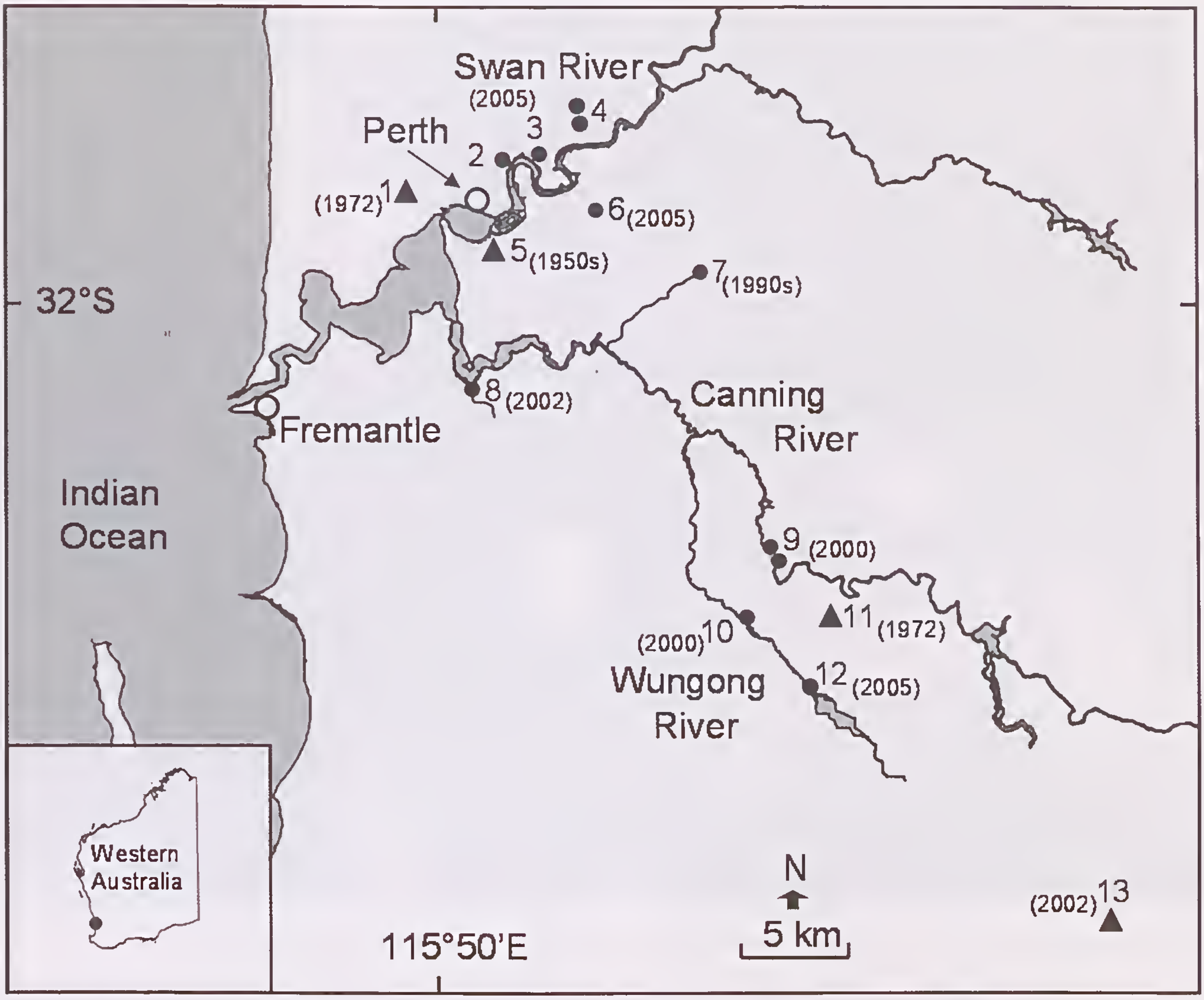

Figure 2. Present (●) and historical (▲) *Phalloceros caudimaculatus* populations within southwestern Australia. Localities (and Perth suburbs) depicted are: 1. Ornamental pond (Subiaco); 2. Banks Reserve drain (East Perth); 3. Mary St drain (Maylands); 4. Mooney St drain (Bayswater); 5. Ellam St drain (South Perth); 6. South Belmont main drain (Belmont); 7. Lesmurdie Brk (Lesmurdie); 8. Bull Crk (Rossmoyne/Bull Creek); 9. Canning River (Kelmscott); 10. Wungong River (Darling Downs); 11. Churchmans Brk (Bedfordale); 12. Wungong Reservoir (Bedfordale); 13. Artificial well, Albany Hwy.

lakes on the Swan River foreshore (Jasper Trendall, Western Australian Fisheries Department, pers. comm.). *Phalloceros caudimaculatus* was observed at South Perth as early as the 1950s, when it was abundant in the drainage system of the foreshore market gardens (Syd Adams, Australian and New Guinea Fish Association, pers. comm.). Recent sampling of drains and ornamental ponds suggests that the species no longer occurs at South Perth, nor at the other location identified by Griffiths (1972), Churchmans Brook (Beatty *et al.* 2003). While the two oldest-known populations in WA appear extinct, *P. caudimaculatus* is now widely dispersed throughout the Swan/Canning system.

Phalloceros caudimaculatus is abundant in Bull Creek and Lesmurdie Brook, both tributaries of the Canning/Wungong system (Fig. 2). It was noted in Bull Creek in 2002 and in Lesmurdie Brook in the 1990s, though the exact date is unclear. Both locations are degraded, urban creeks (Swan River Trust 2002) with *P. caudimaculatus* particularly common in areas with low water flow and littoral vegetation. Both creeks were originally inhabited by *G. holbrooki* but are now dominated by *P. caudimaculatus*. As part of a related research project, *P. caudimaculatus* was collected monthly from both sites between September 2002 and August 2003. *Gambusia holbrooki* was not collected from Bull Creek during the one-year study period, and only 12 adult *G. holbrooki*, compared with c. 6000 *P. caudimaculatus*, were collected at Lesmurdie Brook. Similar observations were made at Long Reef in New South Wales. Rowley *et al.* (2005) noted that between 1997 and 2002 the community structure shifted from one dominated by *G. holbrooki* to one dominated by *P. caudimaculatus*, with *G. holbrooki* "rare or absent". This apparent displacement of *G. holbrooki* by *P. caudimaculatus* has not been observed, thus far, at other locations in southwestern Australia.

Phalloceros caudimaculatus was collected from a number of sites in the Canning and Wungong Rivers,

Figure 3. Author electrofishing for *Phalloceros caudimaculatus* in the Canning River in southwestern Australia.

and adjacent to the Wungong Reservoir (Fig. 2), in 2005. As observed in other waterways, it thrives in areas with structure and/or emergent vegetation that are protected from stronger water flows. Its presence in these systems was noted by Storey *et al.* (2000), however it was not recorded in prior surveys (*e.g.* ARL 1988a; ARL 1988b; Pusey *et al.* 1989; Sarti 1994; Storey 1998). The Canning River (Fig. 3) is the largest watercourse containing *P. caudimaculatus* in this region, and it is inhabited not only by *G. holbrooki*, but also by indigenous fishes including *Edelia vittata* (Percichthyidae), *Bostockia porosa* (Percichthyidae) and *Galaxias occidentalis* (Galaxiidae). Although this study indicated that *P. caudimaculatus* has a restricted distribution within the Canning River, the efficacy of the sampling methodology (*i.e.* hand-held electrofisher) is limited in larger river reaches, as also noted by Storey *et al.* (1998). Whereas Storey *et al.* (2000) recorded *G. holbrooki* as dominant in these systems, *P. caudimaculatus* was marginally more abundant than *G. holbrooki* in the Canning River survey sites (Fig. 2) in July 2005. These findings suggest that a more detailed survey is needed to determine the distribution and prevalence of *P. caudimaculatus* in this system.

The most recent range expansion of *P. caudimaculatus* includes major drainage systems connected to the upper Swan River estuary (Fig. 2). *Phalloceros caudimaculatus* occurs in sections of the Belmont and Bayswater main drainage systems, including the Bayswater artificial wetlands. A survey of the Mary St drain in 2005 revealed both *P. caudimaculatus* and *G. holbrooki* to be abundant amongst emergent vegetation, though the latter species was predominant. A further survey in 2006 indicated that *G. holbrooki* still comprised almost 75% of fish present. In the Banks Reserve drain *P. caudimaculatus* was collected with the estuarine species *Leptatherina wallacei* (Atherinidae) and *Mugil cephalus* (Mugilidae). Although the upper estuary was not surveyed, sampling by Hoeksema and Potter (2006) recorded low numbers of *G. holbrooki* only. *Phalloceros caudimaculatus* may have occurred in ornamental ponds in the suburb of Subiaco (Kevin Griffiths, pers. comm.), though it was not recorded at this location, or at an artificial well southwest of Perth identified in Maddern (2003). Thus, *P. caudimaculatus* is widely dispersed throughout the Swan/Canning catchments in metropolitan Perth and occupies drains and highly modified urban creeks as well as larger rivers, such as the Canning River, that contain endemic ichthyofauna.

Risk of further range expansions in Australia

Further range expansions of *P. caudimaculatus* are likely within southwestern Australia and are determined by environmental and anthropogenic factors. The potential for the "natural" dispersal of the species within the Swan/Canning catchment is increased by the winter hydrological regime of this region which is dominated by large, freshwater pulses (Swan River Trust 2002; Astill & Lavery 2004). During these events, fishes may be flushed from drainage systems (*e.g.* the south Belmont main drain) and tributaries (*e.g.* Bull Creek and Lesmurdie Brook) downstream into the Swan and Canning Rivers, and into adjacent waterways by flood waters. A population of *P. caudimaculatus* within a section of the Canning River indicates that these larger waterways have already been colonised, though the species' distribution appears to be limited to a small section of this river. Thus, even without further human-mediated translocation of fishes, range expansions within the Swan/Canning system appear highly likely, if not inevitable.

Human-mediated translocation is the major vector responsible for the establishment of nonindigenous ornamental fish populations (Arthington & Mackenzie 1997; Lintermans 2004), however the potential for the release of fish is correlated with the popularity of that species and its abundance among fish hobbyists. Although *P. caudimaculatus* appeared to be a popular aquarium species decades ago (*e.g.* Innes 1946; Frey 1970; Axelrod *et al.* 1971; Hoedman 1974) when fewer fish species were available commercially, it was mentioned only once (Sandford 2004) in a brief survey of current aquarium literature aimed at general hobbyists (*e.g.* Mills 1984; Dawes 1987; Stanislav 1992; Bailey & Dakin 1998; Alderton 2003; Evans 2006). *Phalloceros caudimaculatus* was not observed in commercial aquarium outlets in metropolitan Perth in 2005, although it was available from aquarium shops in the past (Kevin Griffiths, pers. comm.). Corfield *et al.* (2007) listed the importance of *P. caudimaculatus* as a commercial aquarium fish species in Australia as "low". The species is kept by hobbyists in NSW (Rowley *et al.* 2005) and is available commercially in Victoria (Anon 2007). Of course, if it is kept as an ornamental species there is always the possibility of release into the wild, although this risk is likely to be less than for more popular, commonly maintained aquarium species.

Phalloceros caudimaculatus may have been translocated and released as a mosquito biocontrol agent in Australia (Arthington & Blühdorn 1995), and Malawi (Denis Tweddle, J.L.B. Smith Institute of Ichthyology, pers. comm.). Ornamental fishes have been released into dams to control mosquitos in Queensland (McKay 1978), and it is reasonable to speculate that *P. caudimaculatus* may have been maintained in outdoor ponds in South Australia (Arthington & Lloyd 1989) for this purpose. *Phalloceros caudimaculatus* is morphologically similar to *G. holbrooki*, a species that is still known as the "mosquitofish" in the wider community. This name is still common despite the fact that the reputation of *G. holbrooki* for controlling mosquito numbers, by consuming mosquito larvae, is considered erroneous (Merrick & Schmida 1984). *Gambusia holbrooki* consumes a wide array of dietary items and rarely eats mosquito larvae if other foods are available (Arthington 1989). Similarly, *P. caudimaculatus* is sometimes referred to as "speckled mosquitofish" or "leopard mosquitofish" (Anon 2007). Thus, this misleading nomenclature and the frequent occurrence of the two species in freshwater habitats may prove a motivation for individuals to collect, translocate and release both species for the control of mosquitos. While conducting field research between 2002 and 2006 in metropolitan Perth, anecdotal reports and direct conversations suggested that *P. caudimaculatus* was irregularly collected from two locations for stocking outdoor ponds and private aquaria, and at least once for commercial profit. Thus, as commented by McDowell (2004), there are individuals in the community who consider nonindigenous fish populations as a harvestable resource rather than an environmental concern. Unfortunately, attitudes such as these will ensure the further translocation and release of introduced ornamental fishes such as *P. caudimaculatus*, and perhaps coincidentally, *Gambusia holbrooki* as well. Aided by natural processes of dispersal such as flooding, it is very likely that *P. caudimaculatus* will continue to spread in Western Australia and possibly also in other areas of Australia.

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Vertebrate by-catch in invertebrate wet pitfall traps

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Abstract

Wet pitfall traps used to sample invertebrates, in particular, short-range endemic invertebrates for the purpose of supporting environmental impact assessments, killed, as by-catch, numerous small vertebrates. For the five surveys reported here, vertebrate by-catch rates varied between 0.4 and 15.6 individuals per 1000 trap nights using two litre plastic containers half-filled with ethylene glycol. No satisfactory alternative trapping strategy is available that provides quantitative data for sampling short-range endemic invertebrates (*e.g.*, terrestrial molluscs, spiders and millipedes), which are a focus of the Western Australian Environmental Protection Authority. We discuss the trade-off between catching short-range endemic invertebrates as part of an environmental impact assessment against killing small vertebrates as by-catch. We urge government environmental regulators to provide greater clarity on the specific locations of where short-range endemic invertebrate surveys should be undertaken as an interim measure for reducing vertebrate trapping deaths until improved trapping protocols are available and to be more cautious when requiring surveys for short-range endemic invertebrates.

Keywords: Short range endemics, reptiles, mammals, birds, fauna surveys

Introduction

Since the release by the Environment Protection Authority (EPA) of Position Statement No 3 *Terrestrial biological surveys as an element of biodiversity protection* (2002) and Guidance Statement No 56 *Terrestrial fauna surveys for environmental impact assessment in Western Australia* (2004), the Western Australian Department of Environment and Conservation (DEC) staff are requiring environmental consultants undertaking fauna assessments for major developments to sample for short-range endemic invertebrates. Much of this work has been stimulated by Harvey's (2002) paper on short-range endemics, which reported a prevalence of Gastropoda, Oligochaeta, Onychophora, Araneane, Schizomida, Diplopoda, Phreatoicidae and Decapoda that had natural ranges smaller than 10,000 km^2, and could therefore be significantly impacted on by large scale land clearing.

Staff in the Western Australian Museum are seen by the Department of Environment and Conservation as the authority on this issue, and environmental consultants are advised to seek their advice on sampling procedures. Museum staff recommended two approaches; hand-collecting and wet pitfall trapping. Wet pitfall trapping involves digging containers into the ground to ground level, and part filling each container with ethylene glycol. Ethylene glycol has a low evaporation rate and therefore lasts for some time. It kills and preserves both invertebrates and vertebrates that fall into the containers.

Wet pitfall traps are routinely used by researchers to sample for invertebrates (*e.g.* Brennan *et al.* 1999; Bisevac & Majer 2002; Andersen *et al.* 2003) and were also used by staff in the Department of Environment and Conservation in their regional biological surveys (Harvey *et al.* 2000; 2004). For example, Harvey *et al.* (2000) used five 300 mm diameter x 450 mm deep traps at each of their 63 sites in the Carnarvon Basin survey, and traps were left open for a period of 12 months (114,000 trap nights). Each container was unfenced, partially filled with a solution of glycol-formalin and covered with a sheet of wire mesh (10 mm square holes). This trapping program caught (and presumably killed) 1,462 individual vertebrates from 87 species of reptiles and amphibians. Subsequently, Harvey *et al.* (2004) used five 2 L pit traps partially filled with glycol-formalin at each of 304 quadrats in the Western Australian wheatbelt. Pit-traps were left open for 12 months to provide 554,800 trap nights of data. Over 6,000 individual vertebrates from 99 species were captured, most of which were presumed to have been killed by the glycol-formalin.

Other researchers have expressed concern about the vertebrate by-catch associated with large scale invertebrate sampling using wet pitfall traps (New 1999; Pearce *et al.* 2005). This paper quantifies the vertebrate by-catch from five invertebrate wet pitfall trapping surveys where a standard protocol was used. As required by the Department of Environment and Conservation, these surveys were undertaken to detect the presence of short-range endemic invertebrates.

Methods

Sites

Five wet pitfall trapping programs aiming to catch short-range endemic invertebrates were conducted at Rockingham (32° 17'S, 116° 00'E), Armadale (32° 07'S, 115° 42'E), Pilbara (22° 18'S, 119° 24'E), Mid-west (29° 35'S, 117° 10'E) and Wiluna (26° 52'S, 120° 10'E) in Western Australia. Trapping occurred for between 58 and 153 nights during autumn, winter and spring with a total of 11600 to 61200 trap-nights for each survey.

There were four broad habitat types at the Rockingham site: Tuart woodland; Melaleuca/Banksia woodland; Acacia/Xanthorrhoea shrubland; and a degraded area that was mostly devoid of vegetation other than grasses. At the Armadale site there were three broad habitat types: open woodland of Marri, Jarrah, Banksia and Melaleuca; open tall forest of Marri, Jarrah and Wandoo; and a mixed low forest of Sheoak, Marri, Wandoo and Jarrah. The five habitat types in the Mid-west were: dense thickets of Mulga (*Acacia* sp.) on ridge tops; dense thickets of Mulga on the sand plain; Mulga woodland on the slopes; open mallee (*Eucalyptus* sp.) scrubland on the sand plain; and, an open mixed woodland on the sand plain. Five habitat types were surveyed at the Wiluna site: salt affected sand plain; sand ridges vegetated with spinifex; Mulga woodland with an understorey of spinifex; Mulga woodland without an understorey of spinifex; and sand plain with scattered shrubs and spinifex. The Pilbara site had three habitat types: thickets of Mulga woodland with an understorey of shrubs; open Mulga woodland with an understorey of shrubs and grasses; and open Mulga woodland with an understorey of grasses.

Wet pitfall traps

Two litre plastic containers (165 mm x 165 mm x 95 mm deep) were dug into the ground so that they were level with the ground surface. Each trap was approximately half-filled with ethylene glycol. Traps were cleared and topped up monthly with ethylene glycol.

Results

The vertebrate by-catch varied among surveyed sites (Table 2, Appendix 1). The highest number of vertebrates caught per trap-night was at Armadale, where 16.6 (15.3 of which were frogs) were caught per 1000 trap nights. *Heleioporus eyrei* was the most commonly caught species (310). Mammals were caught at the Pilbara site (eight *Planigale ingrami*, eight *Mus musculus*, seven *Pseudomys desertor* and one *P. hermannsburgensis*) and at Wiluna (one *Ningaui ridei*), but were not caught at other sites. Birds were only caught at the Pilbara site (four *Taeniopygia guttata*; eight *Malurus lamberti*, two *Malurus leucopterus*, 10 *Coturnix pectoralis*, five *Coturnix ypsilophora* and one unidentified *Coturnix* sp.). Reptiles were caught at all sites and catch rates varied from 0.3 to 3.6 per 1000 trap-nights. Almost all vertebrates caught were dead when the traps were cleared.

Table 1

The trapping period and trapping effort for five wet pitfall trapping programs.

Site	Trapping period	No traps	No nights open	No trap-nights
Rockingham	1/7/ – 28/9/2005	200	90	18000
Armadale	27/4/ – 6/9/2006	200	133	26600
Mid-west	15/4/ – 11/6/2006	200	58	11600
Pilbara	29/4/ – 28/9/2006	400	153	61200
Wiluna	16/7/ – 18/10/2006	200	94	18800
Total				136200

Table 2

By-catch in wet pit-traps at five locations in Western Australia per 1000 trap-nights

	Mid-west	Armadale	Rockingham	Pilbara	Wiluna
Amphibians	2.3	15.3	0.1	0.5	1.6
Mammals	–	–	–	0.4	0.1
Reptiles	1.6	0.3	0.3	3.6	1.1
Birds	–	–	–	0.5	–
All	4.0	15.6	0.4	5.0	2.8

Discussion

Wet pitfall traps designed to catch invertebrates, specifically short range endemic invertebrates, can catch and kill numerous small vertebrates as by-catch. Small birds were only caught in one of the five surveys. In the hot and dry Pilbara, water can be a scarce commodity and it is possible that some small fairy-wrens and quails were tempted to drink the ethylene glycol. Birds that we found were either in the plastic container or nearby. It is unknown if other birds drank from the containers and died some distance away.

In areas where there are a relatively high number of surface active frogs, the wet pitfall traps catch these in relatively high numbers. This was apparent in the surveys in the Pilbara and near Wiluna. The two Department of Environment and Conservation invertebrate surveys referred to above caught in excess of 10 vertebrates per 1000 trap nights. This catch rate was higher than four of the five surveys reported here, with the Armadale survey being higher (Table 2). Frogs made up a high proportion of the catch (58.1%) in the Department of Environment and Conservation Wheatbelt survey and our Armadale survey (98.1%). In arid areas, terrestrial frogs are only surface active after rain. So, in arid and semi-arid areas, if wet pitfall traps are not opened immediately after rain this will reduce the catch rate of frogs. However, this is problematic, as many of the short-range endemics being targeted by these surveys are also more active after rain.

Most of the reptiles caught in wet pitfall traps were small, but occasionally, a large skink (*e.g., Tiliqua multifasciata*) was caught. The comparatively high number of small mammals caught in the Pilbara survey

may reflect either their abundance at this site compared to other sites or small mammals seeking out a source of water in arid conditions. Small mammals were not caught in the mesic areas of Armadale or Rockingham, but this might not be unusual as many of the small native mammals (perhaps with the exception of *Mus musculus*) are no longer present on the Swan Coastal plain near human habitation (How *et al.* 1996).

In recent years, the Western Australian Environmental Protection Authority (2004) has taken a keen interest in the possible presence of short range endemic invertebrates in development areas. The consequence is that environmental consultants are often required to undertake surveys of invertebrates as part of the terrestrial fauna surveys to support environmental impact assessments lodged by developers seeking government approval for vegetation clearing and ground disturbance. However, although the EPA indicated that Guidance Statement No 56 provides guidance on the standard of survey required, the document is silent on how to undertake surveys for short-range endemics, and EPA staff advise environmental consultants to take the advice of the Western Australian Museum. Invertebrate surveys reported here were undertaken in accordance with the general advice provided by the Western Australian Museum staff. It is understood the EPA is intending to release a Guidance Statement relating to surveying short-range endemic invertebrates.

The EPA is rightly concerned about protecting short-range endemic invertebrates from developments and vegetation clearing. However, if vertebrates are being killed as by-catch in these surveys, then there is a trade-off between identifying and protecting short-range endemic invertebrates and killing vertebrates in the process of detecting their presence in an area. The level and intensity of surveys for short range endemic invertebrates, and thus the number caught, must therefore be traded-off against the killing of small vertebrates caught as by-catch.

The Western Australian Animal Welfare Act (2002) indicates that a person must not use animals for scientific purposes unless they belong to a scientific establishment that holds a licence authorising the use of animals. The Act makes no mention of environmental consultants, and most currently do not seek animal ethics clearances for their field surveys. However, elsewhere in Australia, environmental consultants undertaking fauna surveys are required to obtain approval from an animal ethics committee. Although the legislative requirements in most Australian states are similar (see http://www.raa.nsw.gov.au/reader/arrp-legislation/other-aust-leg.htm) it is not clear whether environmental consultants require ethics approval in Western Australia to undertake fauna surveys or whether it does not occur because there is no mechanism to assess applications.

New (1999), in his editorial for the Journal of Insect Conservation, raised the ethical issue of the small number of frogs and juvenile skinks being caught in wet pitfall traps used to survey invertebrates. He went on to suggest that invertebrate surveyors would probably need to obtain animal ethics committee approval before they undertake wet pitfall trapping for invertebrates. The most recent edition of the Australian Code of Practice for the Care and Use of Animals for Scientific Purposes (2004) indicates that wet pitfall traps used to capture invertebrates must be managed to minimise the inadvertent capture of vertebrates. As yet, there is little information on what strategies or protocols might be employed to minimise vertebrate catches.

From an ethics perspective, if the vertebrate by-catch during invertebrate surveys is low, then the administrative burden associated with obtaining approvals and reporting the by-catch would suggest that the current arrangements are appropriate. In the scenario where there is little concern about current practices, then the stimulus to develop strategies and protocols to reduce vertebrate by-catch will be weak. However, if vertebrate catch rates are high, then there may be a compelling case to devise alternative protocols to sample invertebrates, and government officials might be more circumspect in recommending large scale invertebrate surveys when the justification for these surveys is not strong.

Is there a potential to modify the size, placement or type of wet pitfall traps to minimise vertebrate by-catch? Pendola and New (2007) recommended the use of shallower pitfall traps (15 vs 8 cm deep) for sampling invertebrates on the basis that the shallower traps were less likely to catch vertebrate by-catch. However, they were not able to demonstrate this difference in by-catch because they caught no vertebrates in either trap depth. Borgelt and New (2005) suggested that that smaller diameter test-tube type traps (ca 18mm) can be as effective as the wider (coffee cup) traps (ca 70mm) to sample for broad inter-treatment comparisons of on ants. However, ants are rarely the focus of short-range endemic invertebrate investigations in Western Australia, but these smaller diameter traps may also catch few of the targeted short-range endemic invertebrates (see Work *et al.* 2002). Lemieux and Lindgren (1999) compared the use of 1 L pitfall traps and Nordlander traps made from the same containers and reported that the cover over the trap and the restricted entrances to the Nordlander traps were superior to the pitfall traps in excluding small vertebrates. This investigation only considered Carabidae (beetles), and it is not known whether the Nordlander traps would be effective in trapping a range of short-range endemics, nevertheless, the issue is worthy of further investigation. Karraker (2001) examined a novel trapping strategy of attaching twine to the undersides of cover boards over pit-traps to provide an escape route for mammals to minimise the vertebrate mortality in pitfall traps. This twine might also be effective in enabling some smaller reptiles to escape.

Other possible solutions include not using a liquid to kill the invertebrate catch (see Thompson and Thompson 2007). However, in the Thompson and Thompson (2007) investigation, it was not known what invertebrates escaped from the PVC buckets by climbing up the sides, as some species of terrestrial mollusc, spider and millipede will readily climb out of pitfall traps. Placing a lid over the trap to limit the height of individuals able to pass between the lid and the lip of the pitfall trap is another possible solution. This might stop birds and perhaps some mammals and the larger lizards (*e.g., Tiliqua multifasciata*) from being caught. However, it may also restrict entry into the pitfall trap by molluscs and beetles. The cover might also provide temporary shelter for small reptiles which would become caught.

Pearce *et al.* (2005), concerned about the by-catch associated with wet pitfall traps, examined the potential to use alternative trap types to catch epigeal invertebrates (*e.g.*, Carabidae, Staphylinidae, millipedes, centipedes and woodlice). They used conventional pitfall traps, funnel pitfall traps, shallow pitfall traps, Nordlander traps and ramp traps in a mixed forest in Ontario, Canada and reported that vertebrate captures (mammals and amphibians) were significantly less in the four alternatives to pitfall traps. Carabid beetle catch rates varied among trap types, but were highest in the normal pitfall trap. The ramp trap appeared to sample a different component of the spider assemblage compared to the other trap types. Most spiders were caught in the ramp traps, and the funnel traps caught the fewest individuals and species of spider. This report suggested that alternative trap types could be used to effectively sample terrestrial invertebrates, and the use of alternative traps may reduce the vertebrate by-catch.

Another alternative that may be suitable in some situations is to collect leaf litter samples in the field and using either Berlese or Tullgren funnels, sort the invertebrates from the litter. Transporting large samples of leaf litter to the laboratory and adequately sampling the area are two problems that need to be addressed with this alternative, but it will probably reduce the number of vertebrates killed in wet pit-traps.

The obvious solution to reducing vertebrate by-catch is to only trap for invertebrates when the data are essential, and to limit the period wet pitfall traps are be left open.

In the absence of clear guidelines on when, where and how short range endemic invertebrates should be sampled as part of environmental impact assessments, we urge government environmental agencies to be more cautious in requiring that invertebrate fauna surveys be undertaken for short-range endemics, when there is little evidence to suggest that proposed developments will have a significant impact on these invertebrates (*e.g.*, when the disturbance area is small, or represents a small fraction of the available undisturbed habitat). We would also urge the EPA to revise its Guidance Statement No 56 *Terrestrial fauna surveys for environmental impact assessment in Western Australia* (2004) and to clearly indicate in what circumstances, geographical areas and habitat types surveys for short range endemics are required, and the protocols and intensity of the survey effort that is considered appropriate.

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Appendix 1

Species of vertebrates caught as by-catch during the five surveys for short range endemics

	Family	Species	Mid-west	Armadale	Rockingham	Pilbara	Wiluna
Amphibians	Hylidae	*Litoria rubella*				29	
	Myobatrachidae	*Crinia georgiana*		12			
		Crinia sp.		48			
		Heleioporus eyrei		310	1		
		Limnodynastes dorsalis		35			
		Neobatrachus sutor	21				
		Neobatrachus wilsmorei	6				31
		Pseudophyrne guentheri		2			
Birds	Estrildidae	*Taeniopygia guttata*				4	
	Maluridae	*Malurus lamberti*				8	
		Malurus leucopterus				2	
	Phasianidae	*Coturnix pectoralis*				10	
		Coturnix sp.				1	
		Coturnix ypsilophora				5	
Mammals	Dasyuridae	*Ningaui ridei*					1
		Planigale ingrami				8	
	Muridae	*Mus musculus*				8	
		Pseudomys desertor				7	
		Pseudomys hermannsburgensis				1	
Reptiles	Agamidae	*Caimanops amphiboluroides*				2	
		Ctenophorus caudicinctus				8	
		Ctenophorus isolepis				13	1
		Ctenophorus reticulatus				1	
		Ctenophorus scutulatus	6				2
		Pogona minor		1	1		
		Pogona mitchelli				5	
		Rankinia adelaidensis			2		
		Tympanocryptis cephala				1	
	Elapidae	*Brachyurophis semifasciata*					1
	Gekkonidae	*Diplodactylus conspicillatus*				10	
		Diplodactylus pulcher				8	
		Diporiphora winneckei				1	
		Gehyra sp.				1	
		Gehyra variegata				1	
		Heteronotia binoei	1			7	
		Lerista muelleri	3				
		Lichenostomus virescens				13	
		Nephrurus wheeleri				2	
		Lucasium maini	2				
		Rhynchoedura ornata					1
		Strophurus elderi				1	3
		Strophurus spinigerus			1		
		Strophurus strophurus					1
		Strophurus wellingtonae				4	
	Scincidae	*Cryptoblepharus plagiocephalus*		7			
		Ctenotus helenae				12	4
		Ctenotus leonhardii					3
		Ctenotus pantherinus				22	1
		Ctenotus saxatilis				25	
		Ctenotus schomburgkii	6				
		Ctenotus sp.				26	
		Egernia inornata	1				
		Lerista desertorum					2
		Lerista elegans				7	
		Lerista muelleri				48	1
		Lerista sp.				1	
		Menetia greyii			1	1	
		Morethia obscura			1		
		Tiliqua multifasciata				1	
	Typhlopidae	*Ramphotyphlops* sp.				1	
	Varanidae	*Varanus bushi*				1	

The Western Australian soldier crab, *Mictyris occidentalis* Unno 2008 (Brachyura: Decapoda: Mictyridae): the importance of behaviour in design of sampling methods

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Abstract

Soldier crabs are challenging marine organisms to sample as they do not fit neatly into established faunal behavioural categories. Information on the soldier crab life cycle, ichnological products, and behaviour is a prerequisite to designing appropriate sampling, involving the consideration of the study objective (what to sample), temporal factors (when to sample), spatial factors (where to sample) and sampling method (how to sample). Largely infaunal for most of their life cycle, soldier crabs may be relatively sessile or quite vagile within the substrate, and epifaunal (emergent) for late stages of their life cycle. They also exhibit population partitioning, based on sex and size classes (when there are mixed cohorts); for example, it is mostly adult males that emerge in swarms, and mainly females and juveniles that remain in the subsurface. This behaviour has implications for studies of population dynamics that involve abundance, population structure, and sex ratios. To date, there has been emphasis on sampling while the crabs are emergent (forming so called "armies", or surface swarms), with the assumption that the whole population emerges. When infaunal and mobile, soldier crabs also present challenges to sampling in that they can vary in abundance laterally and vertically in a short time, and they can respond to prolonged sampling, or to researcher-induced perturbations during sampling, by burrowing downwards to avoid being collected (resulting in potentially spurious data with respect to their depth of occurrence and abundance). The complexity in behaviour of soldier crabs, the partitioning of populations, and the response to sampling have not been addressed to date by researchers elsewhere whereas it is an important component in the design of sampling methods.

Keywords: soldier crab, *Mictyris occidentalis* Unno 2008, sampling, crab behaviour, north-western Australia

Introduction

Sampling strategies and methods for marine benthic macroinvertebrates depend on the specific objectives of the study which may range from collections for taxonomic, biogeographical, and physiological studies, to quantitative ecological studies describing population dynamics including abundance, size, and distribution, as well as aspects of life history such as reproduction, recruitment, and mortality. For quantitative studies, accuracy and robustness of results and hence the correctness of conclusions derived from interpreting these data depend on the use of sampling strategies and methods appropriate for the type of organism being sampled, the nature of the organism's habitat and the sampling effort (number of replicates). For a given species, sampling strategies or protocols involve the design of a sampling program, *i.e.*, when, where and how to sample, and use of methods involving particular equipment and techniques appropriate to the objectives of a study. Traditional sampling strategies may include use of random quadrats, or sampling at regular intervals along transects, *etc.* Traditional sampling methods include the use of equipment such as sweep nets, suction devices, grab samplers, dredges and cores. While there have been several examples of generalised sample design (Green 1979; McIntyre *et al.* 1984; Clark & Green 1988; Riddle 1989; Underwood 1997; Underwood & Chapman 2001), and studies of methods for collecting benthic organisms (Holme 1964; Boudouresque 1971; Parker 1975; Ankar *et al.* 1979; Warwick & Clarke 1991; Eleftheriou & McIntyre 2005) in the literature, this paper is the first to describe a sampling strategy and methods specifically for the Western Australian soldier crab *M. occidentalis* Unno 2008, designed in response to information on its life stages and its behaviour. These methods, in fact, are applicable to some degree to other species of *Mictyris.*

Speciation within a genus can result in behavioural differences between the taxa. The species of fiddler crab, *Uca*, exemplify this: with over 50 species of *Uca* worldwide, each species exhibits differences in habitat preferences, depth of burrowing, shape of burrows, and other behavioural characteristics (Crane 1975). At present, there are five species of *Mictyris* described in the Indo-Pacific region (Davie 2002; Unno 2008), and while there are similarities in behaviour between them, it is not to be unexpected that speciation could result in

differences in behaviour and habitat preferences of the various taxa within this genus. Thus, while the results of this paper are specifically directed to the sampling of *M. occidentalis*, the principles of adjusting methods to be appropriate to the behaviour of the Western Australian soldier crab, described herein, at the least, can be applied to other species of *Mictyris* in the Indo-Pacific region in that generally there is enough overlap and similarity in the behaviour of the various species, though not necessarily in detail.

The Western Australian soldier crab, *M. occidentalis*, is infaunal to epifaunal and is behaviourally a complex organism (Unno & Semeniuk 2008), and this can result in difficulty in its sampling and ambiguity in a given set of results deriving from sampling. If the complex crab behaviour is not addressed, sampling is likely to result in data that are incomplete, or that are artifacts, spurious, biased, or ambiguous.

In general, for any macroinvertebrate on tidal flats, where studies of abundance, population dynamics, and population structure are undertaken, information on the whole subpopulation, under or on the area of tidal flat being sampled, is required, *i.e.*, for a given area of sampling, all crabs need to retrieved. Further, if a portion of a population becomes emerged (epifaunal), for valid intra-population comparisons of abundance, size classes, and sex ratios, the emergent and infaunal components of the subpopulation need to be sampled concurrently.

Specifically for *M. occidentalis*, since this species spends most of its life cycle as infauna, and emerges generally during the late stage of its life, there can be problems in sampling the populations. Further, its behaviour, whether infaunal or emergent, is variable, and spatially and temporally patchy. For instance, if any adult crabs emerge, there is a proportion of the crabs that may remain in the subsurface. This is particularly so if the population is composed of mixed stages of cohorts, but also is the case even if the population is composed of a single adult-sized cohort. Additionally, even if remaining wholly in the subsurface, the population also may behave variably, with patches working the sediment as near-surface infauna, and other parts of the population remaining inactive (Unno & Semeniuk 2008).

This paper reports on the variety of behaviour of the Western Australian soldier crab *Mictyris occidentalis* Unno 2008 with regard to the way it has responded to various sampling techniques, and in relation to the problems that may arise if researchers do not address soldier crab behavioural variability, with a view to describing the best sampling methods for the soldier crab during various stages of its life cycle.

This paper is structured as follows:

- description of the complex and variable behaviour of *M. occidentalis*
- review of soldier crab sampling methods in the literature
- implications of soldier crab behaviour for sampling strategies and methods
- sampling methods investigated in this study
- results of various sampling methods employed in this study
- conclusions and recommended strategies and methods for sampling soldier crabs

This work is based mainly on three study sites along the Western Australian coast: King Bay (Dampier Archipelago), Settlers Beach (near Cossack), and Broome (Fig. 1A), and detailed work in the Dampier Archipelago (Fig. 1B).

In this paper, the term "box core" is used for a metal open-ended box, with square cross-section, used for coring sediment; "cylindrical core" is a term used for circular pipes, usually of polyvinyl chloride (PVC), but also of metal; and "spading" is used describe the excavation of sediment by spade usually from inside a marked quadrat.

Complex and variable behaviour of *M. occidentalis*

Behaviour of the Western Australian soldier crab on the tidal flat, particularly in relation to the various ichnological products generated by the crab, is linked to its life cycle. Excluding its marine larval stage, the soldier crab life cycle can be divided into three stages: the early, post-settlement stage where the crab has a carapace length of 1–3 mm; the middle, juvenile stage with a carapace length between 3–7 mm; and the late, adult stage with a carapace length of 7–17 mm. This post-larval life cycle takes about twelve months from recruitment to an adult size of 12 mm carapace length.

Throughout most of their life stages the crabs are largely infaunal, maintaining a subsurface air bubble, and can migrate horizontally or vertically through the substrate in this cavity (Unno & Semeniuk 2008). The early, post-settlement stage crab generally is entirely infaunal – the only ichnological clue to its presence is a tiny "clot" of sand on the sediment surface, the result of subsurface feeding and burrowing activities. Juvenile and adult females also are largely infaunal, producing a range of ichnological products as a result of their feeding and burrowing activities, including singular pustular structures, tunnel structures and pustular mats as well as subsurface structures such as air-filled elongate to circular cavities 1–2 cm in diameter (Unno & Semeniuk 2008). Crabs producing pustular structures during a low tide, can be daytime or night activity. Based on aquarium studies, supplemented by field observations immediately after a receding tide, Unno & Semeniuk (2008) documented soldier crabs moving their air bubble cavities deeper into the sediment during high tide, to avoid predators, and during low tide, moving close to the surface to commence feeding activities. If the crabs remain infaunal in the near-surface, these feeding activities produce discard pellets which are pushed to the surface, accumulating to form pustular structures and tunnel structures which, over the course of the low tidal period, may form an agglomerated pustular mat structure of sediment workings spread over large areas of the tidal flat. An index, then, of the crab population proximity to the very near-surface is the appearance of a mat of pustular structures (Unno & Semeniuk 2008). In the aquarium, the crabs remained in a zone 10 cm from the sediment surface for simulated low tide and high tide (Fig. 2).

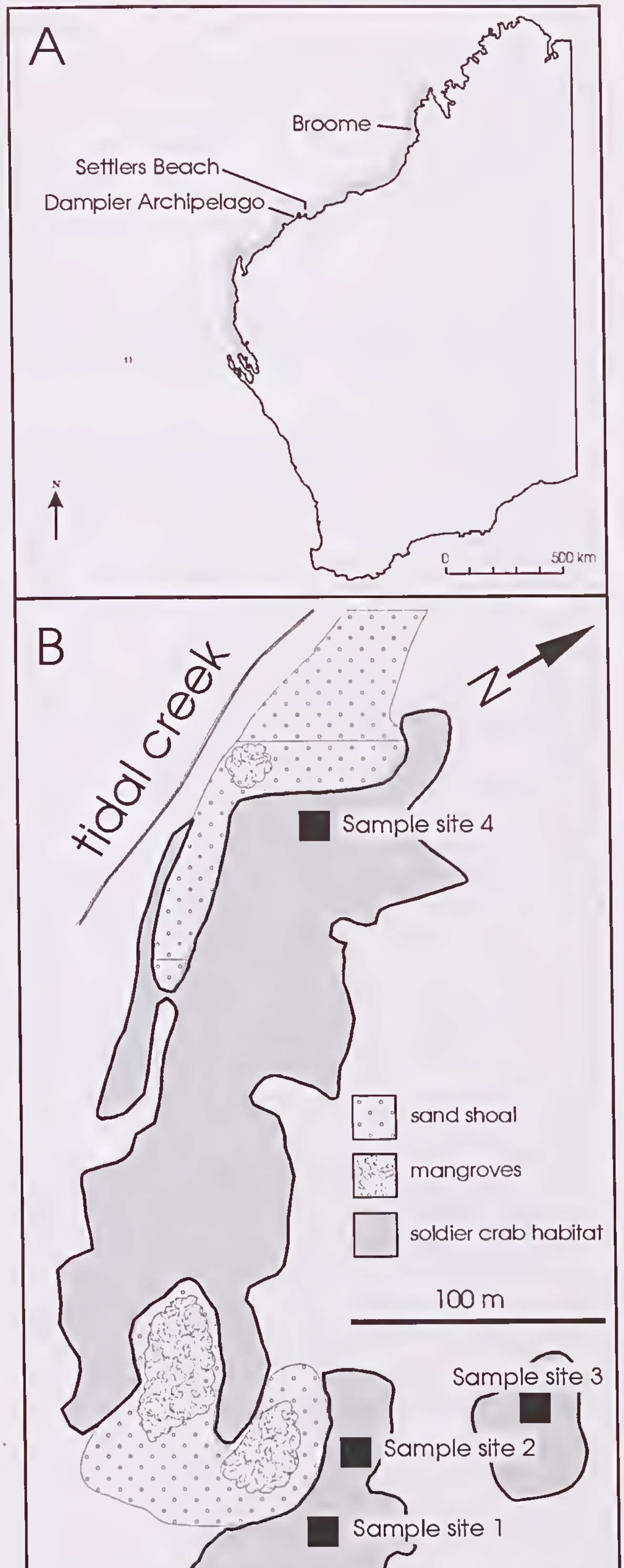

Figure 1. Location map and sampling sites. A. Sampling localities along the coast in Western Australia. Grey border to coast shows the biogeographic extent of *Mictyris occidentalis*. B. Soldier crab habitat (after Unno & Semeniuk 2008) and sampling sites in King Bay, Dampier Archipelago.

When the crabs are in their late adult stage, during some low tidal periods, adults (mostly older blue males) may emerge, forming a swarm, and move about the surface, feeding, and leaving a pelleted surface of discard pellets (Unno & Semeniuk 2008). During this late adult stage, the population may also exhibit a temporary phase of not swarming. When a swarm commences, hundreds of individuals may emerge and feed, but generally do not interact, moving in fact randomly over the tidal flat. However, if a predator (or a human who is perceived as a predator) appears, each individual crab will move in the direction away from the predator, producing an effect that appears to be movement in concert as occurs in an "army". When emergent, adult crabs produce exit holes, craters and rosettes.

The behaviour of *Mictyris occidentalis,* whether infaunal or emergent, is variable, hence activity occurs in a patchy manner. For instance, for every emergence of crabs, there is a proportion of the crabs that may remain in the subsurface. This is particularly the case if the population is composed of mixed stages of cohorts, but also the case even if the population is composed of a single cohort. If remaining wholly infaunal (*i.e.*, remaining in the subsurface), the population also may behave variably, with patches of workings appearing on the sediment indicating near-surface infaunal activity, and other parts of the population remaining lower in the substrate with no surface expression of their activities (*cf.* Figures 8 and 9 of Unno & Semeniuk 2008).

Subsurface activity of infaunal soldier crab populations is variable from day to day with some crabs moving horizontally or vertically through the substrate while others remain relatively inactive. The habitual, undisturbed depth of occurrence in the substrate of the soldier crab is best observed in aquarium studies and is generally between 0 cm and 15 cm (Unno & Semeniuk 2008).

Review of soldier crab sampling methods

A basic prerequisite for present and future comparisons of the various behavioural activities, population dynamics, and partitioning of soldier crab populations in terms of their life stage and sex, is that comparable data are/were collected for the various species of *Mictyris*. To this objective, the various sampling methods for the species of *Mictyris* worldwide were reviewed to provide an assessment of the reliability of the data and information in the literature.

Various aspects of the species *of Mictyris* in the field and in the aquarium have been described in papers from South-east Asia and Australia. Topics for study have included: taxonomy and biogeography (Alcock 1900; McNeill 1926; Takeda 1978; Unno 2008); physiology (Quinn 1980; Sleinis & Silvey 1980; Kraus & Tautz 1981; Maitland & Maitland 1992); ontogeny (Cameron 1965; Fielder *et al.* 1984; Fukuda 1990); ichnology (Unno & Semeniuk 2008); feeding (Quinn 1983); reproduction (Nakasone & Akamine 1981; Takeda 2005); population dynamics (Shih 1995; Dittmann 1998); behaviour (Cameron 1966), and ecology (Cowles 1915; Rossi & Chapman 2003; Webb & Eyre 2004). Most of these

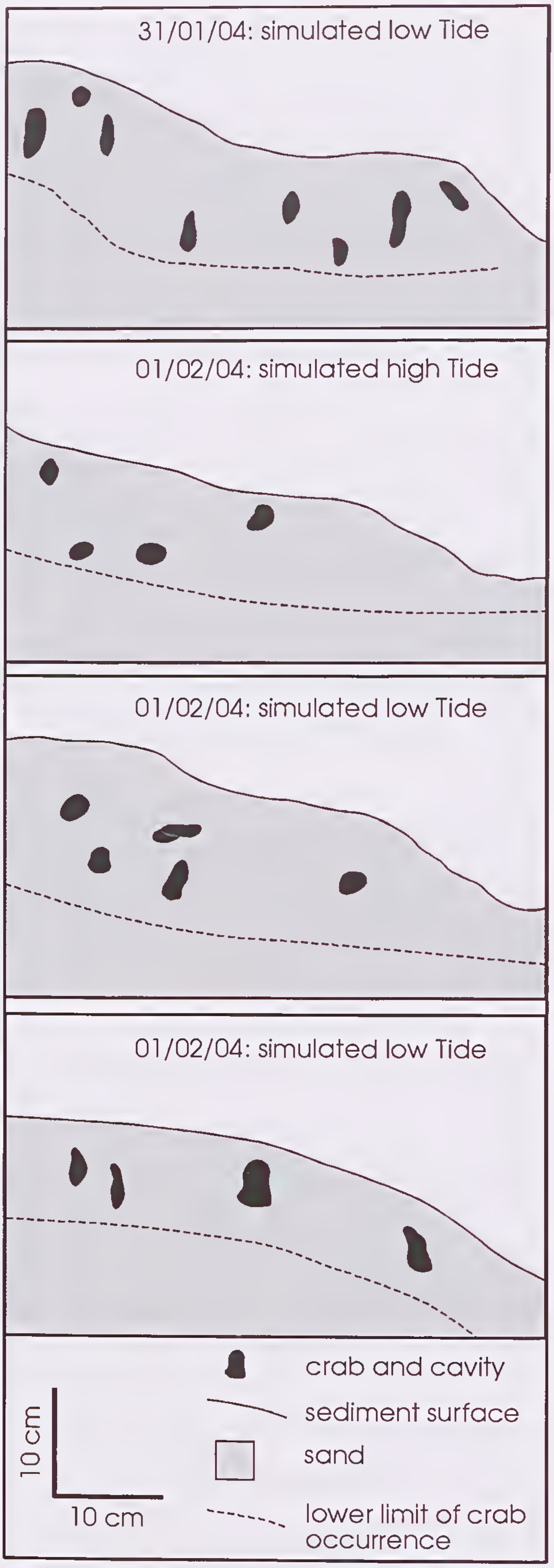

Figure 2. Occurrence of crabs and their subsurface cavity under simulated high tide and simulated low tide conditions in the aquarium. The crabs occur within a topography-conforming zone within 10 cm of the surface.

papers, however, do not describe in detail the sampling methods employed to collect crabs.

A selection of key research papers on soldier crabs that do describe, imply or allude to sampling methods for collection of crabs are reviewed below, with a focus on sampling methods for crabs in their natural tidal flat environment, and the sampling methods therein assessed using criteria, when appropriate, as to whether the sampling appeared to achieve the objective of the paper, whether the whole population or partial population actually was collected, and whether disturbance during sampling possibly triggered a reaction in the crab to "escape from a predator" such that the results were inadvertently biased.

The early work on soldier crabs was taxonomic and involved qualitative observations of burrowing style and burrowing depth. Cowels (1915) focused on the habits, feeding and burrowing behaviour and the ichnological products of *M. longicarpus* Latreille, 1806 in the Philippine Islands (a taxon now assigned in that region to *M. brevidactylus* Stimpson, 1858), including the production of subsurface cavities. Cowles (1915) excavated to at least ~ 10 cm to study the crab (actual depth was not reported but can be estimated from Figure 3 Plate II of Cowles 1915). Information of direct relevance to this paper is that the soldier crab *M. brevidactylus* burrows to a depth of at least 10 cm, and that it undertakes what I term "predator avoidance" by rapidly burrowing.

In a largely taxonomic paper, McNeill (1926) anecdotally described the occurrence and habits of various species of *Mictyris*, drawing on notes and comments of collectors for *M. livingstonei* McNeill, 1926 and *M. platycheles* H Milne Edwards, 1852, but provided direct information/descriptions of the behaviour of *M. longicarpus*. From opportunistic collection in the Botany Bay region from swarms, and supplementary sampling by excavations by spade, McNeill (1926) describes *M. longicarpus* as occurring in the subsurface to depths of 5–9 inches (~ 15–22 cm).

Cameron (1966) reported on visual and filmed observations of swarms of *M. longicarpus* carried out from a hide on the tidal flat. Although primarily a study of swarming behaviour, excavations by spade also were carried out for qualitative determination that there were soldier crabs in the subsurface at the same time that the crabs were swarming. Cameron (1966) confirmed McNeill's (1926) observations that predominately male soldier crabs comprise the swarm but does not describe the method used for this observation/conclusion.

Nakasone & Akamine (1981) described the reproductive cycle of the soldier crab and the growth of juveniles over a year for *M. brevidactylus*, collecting crabs by excavating 50 cm x 50 cm quadrats (reducing the quadrat size to 25 cm x 25 cm if large numbers of juveniles were present) and sieving the sediment through two mesh sizes (a 2 mm mesh, and later, a 10 mm mesh). Depth of sampling was not recorded in the description of the methods. Also, the actual method of excavation was not described in detail, although it is unlikely that a box core with such large 50 cm sides would have been used, and it would seem probable that the quadrat size was a marked area on the tidal flat to delineate the area of

excavation. The reported population structure may have been inaccurate due to incomplete collection of crabs. Juvenile recruits < 2 mm would not have been collected in this study. Large adults may also have been under-represented in the reported population structure for subsurface crabs due to the sideways or downward escape movements (see later). No sampling of the subsurface population occurred at the same time as the collection of swarming crabs.

In collecting crabs for physiological studies in the laboratory of the functioning of the lungs of soldier crabs, Maitland & Maitland (1992) reported on the behaviour and burrowing activities of *M. longicarpus* in Botany Bay, and noted that they accorded with the observations of earlier authors. In their own collecting methods, Maitland & Maitland (1992) excavated soldier crabs with a spade to 30 cm, and observed that the crabs occur between 10–30 cm below the sand surface. The disturbance of the sediment due to excavation by spade may have driven the crabs to deeper levels, therefore the maximum depth of 30 cm may not represent the normal habitation level of the soldier crabs.

Shih (1995) undertook a study of the population densities and annual activities of *M. brevidactylus* in Taiwan, providing data on abundance, growth rates, egg-carrying period of the female, and sex ratios. The paper is confusing in the description of methods because while a quadrat 1 m x 1 m x 0.2 m was excavated to retrieve the crabs, the author describes (manually) collecting only obviously visible crabs > 4 mm in size, yet population structures presented in Figures 3 and 4 of Shih (1995) show that animals from 1 mm to 15 mm were apparently collected. The methods make no mention of sieves or sieve sizes involved in the study, though it would be difficult to manually collect crabs in the 1–4 mm size range, and so it must be concluded that a sieve probably was used. Sediment disturbance was not accounted for. The quadrats to sample the subsurface population were relatively large (1 m x 1 m) and would have taken some time to excavate, thereby increasing the chance that the crabs might have escaped by burrowing out, or burrowing deeper to avoid collection by the "predator" researcher. Whether the species naturally occurred at depths > 20 cm, or whether the animal burrowed to depths > 20 cm to avoid collection, is not known, and hence the data on population structure and sex ratios may be biased or incomplete, and as such, the results of Shih (1995), at this stage, should be viewed as potentially spurious or ambiguous.

Dittmann (1998) undertook studies on the behaviour and population structure of *M. longicarpus* in Queensland, collecting crabs from swarms for sex ratios and size class measurements. Sex ratios and size classes were estimated for emergent crabs only, and the structure of the subsurface population under the swarm was not addressed, and hence the true whole-of-population structure had not been documented, and the sex ratio of the whole-of-population also had not been documented. This is an example of the focus on the very obvious swarms on the tidal flat surface with the assumption that the whole population swarms at the same time.

Rossi & Chapman (2003) studied the influence of sediment on burrowing by the soldier crab *M. longicarpus* in Port Jackson and Botany Bay in New South Wales. Abundances were determined by counting crabs collected from sediment excavated from plots 30 cm x 30 cm x 20 cm deep (presumably by spade or similar tool), and sieved through a 2 mm mesh. The authors observed from preliminary diggings that soldier crabs generally excavate the sediment to a depth of 15 cm and selected the plot size for ease of removal with minimum disturbance. Results for abundance and size classes for this study would be accurate for the > 2 mm sized crab population, due to the smaller quadrat size.

In a study of *M. brevidactylus* in Japan, Takeda & Murai (2004) undertook observations on soldier crab feeding behaviour in relation to water levels, and determined abundance and size class measurements as well as sex ratios. They primarily focussed on collecting crabs from swarms and only once concomitantly from the subsurface by excavating 5 blocks of sediment 50 cm x 50 cm x 30 cm deep (presumably by spade – the exact method is not mentioned, but sampling a quadrat 50 cm x 50 cm in size would suggest a quadrat marked on the tidal flat surface and excavated, rather than a large metallic box core to core the sediment). Sediment disturbance is not accounted for since the subsurface population sampling quadrats were relatively large, and would take some time to excavate, thereby increasing the chance of crabs escaping by their sideways or downward mobility. As with Shih (1995), excavating soldier crabs in such large quadrats to a depth of 30 cm similarly would have run the risk that the animals may have burrowed deeper and sideways to avoid collection by the "predatory" researcher. As such, the results of Takeda & Murai (2004) at this stage, similar to the results of Shih (1995), also should be viewed as potentially spurious or ambiguous as the data on population structure and sex ratios may be biased or incomplete.

Takeda (2005) sampled soldier crabs in a study of sexual differences in behaviour during the breeding season of *M. brevidactylus* in Japan. This was not a study of population structure, and as such Takeda (2005) retrieved animals, after they had ceased their surface activities (emergences), only from a quadrat 50 cm x 50 cm to 20 cm depth, over an area where there were soldier crab surface workings (term from Unno & Semeniuk 2008). The description of the methods employed by Takeda (2005) suggests that the 50 cm x 50 cm quadrat was placed (or marked) on the surface to mark the area for excavation only and was not an open-ended metal box (a box core). The sand excavated was washed though a 2.5 mm sieve to collect the animals.

Interestingly, with the same species, *M. brevidactylus*, Shih (1995) and Takeda (2005) both excavated sediment to depths of 20 cm, while Takeda & Murai (2004) excavated to depths of 30 cm. If the crab occurs to depths of 30 cm, Shih (1995) and Takeda (2005), in fact, did not fully retrieve all animals in a given quadrat, and if the animal burrowed to depths > 30 cm, the three studies did not fully retrieve all animals in the study quadrats. If during sampling, the animals were undertaking "predator avoidance" behaviour, and burrowed even more deeply, then Shih (1995), Takeda & Murai (2004) and Takeda (2005) have under-sampled the soldier crab populations.

All methods of sampling described above did not seem to make allowance for crabs burrowing deeper to avoid "researcher predation" and so the maximum depths recorded for observed occurrence of soldier crabs may be an artifact of sampling procedure. In the study by Takeda & Murai (2004), the population numbers may be also be artifacts if the authors did not account for possibility of rapid lateral migration by the crabs to avoid predation. In the studies by Dittmann (1998), only surface swarms were collected, and as will be described later, these may provide a biased sample of the total population size classes and sex ratios if the subsurface crabs were not sampled. Only Rossi & Chapman (2003) appear to have addressed the importance of not disturbing the sediment during excavation of quadrats.

A problem with all the sampling that involved excavation of a quadrat, particularly where the water table is near the surface, is that the sides of a 20 cm or 30 cm wall of sand will collapse, and crabs residing in the sand adjoining the quadrat will slump into the excavation, or migrate in the subsurface into the excavation (see later). In this context, it is important to have a wall that supports the sides of the excavation, *i.e.*, the side of a metal box (a box core), or the side of a large diameter pipe (a cylindrical core).

Implications of soldier crab behaviour for sampling strategies and methods

From the literature, and from field work in northwestern Australian, it is evident that to obtain robust data on population dynamics and sex ratios, sampling of *Mictyris* must involve infauna populations as well as swarms, and must address a number of issues.

The first is 'where to sample'. As vagile organisms, patches of soldiers crabs do not always occur in the same area within the habitat. Sampling within a fixed area within the habitat of size, say, 5 m x 5 m, marked by posts, may result in variable numbers from week to week, or month to month, not reflecting changes in abundance, but the variation in density due to internal adjustment of the density of the population. These types of results, of varying abundance in time reflecting an internally temporally changing density, contrast with organisms such as infaunal bivalves, that may remain resident within a patch of habitat for months, or fiddler crabs, that remain in relatively fixed burrows for weeks and months. Thus, sampling in the same fixed location may provide results showing variation in population density, but this may only be reflecting the very localised immigration and emigration of individuals into and out of the fixed sampling site.

The use of pustular structures as evidence of the crabs in the near-surface is an indicator of the occurrence of crabs in the subsurface within the habitat, or within a fixed sampling site. However, pustular structures are variable in occurrence and density on a tide by tide basis (Figure 9 of Unno & Semeniuk 2008).

The second is 'how deep does the crab burrow. When it is necessary to obtain samples of populations to determine density, density variations, size classes, and sex ratios, it is important to know that the entire subpopulation has been retrieved. Sampling to 10 cm depth by coring, if the crab is burrowing from near-surface to depths of 40–50 cm depths, clearly will produce a biased and inaccurate estimate of abundance, size classes, and sex ratios.

There have been conflicting results about the depth of occurrence of soldier crabs within the substrate and hence how deep to sample to retrieve a representative sample of the population. Sampling of the Western Australian soldier crab shows that the species responds to the sampling regime as though the researcher were a predator, *i.e.* the crab digs deeper into the sediment in an escape response (see later). The depth of occurrence of the crab during sampling often is a function of (or a bias reflecting) sampling style, *e.g.*, slow incremental sampling may drive the crab to deeper depths to avoid what it may perceive as proximity of a predator. Hence, while Maitland & Maitland (1992) reported that the soldier crab was found at a depth of 30 cm, in this instance it appeared that the crab may have been retreating from anthropogenic excavating activity. Ascertaining the normal habitation range of the soldier crab within the substrate and therefore the required length for sample cores should be an important objective of any ecological study.

Thirdly, given that the adults are the main size class that swarms, and that mid-aged individuals, juveniles, and settlement phase individuals largely remain in-faunal, the next group of issues are: 'what proportion of the population swarms', and 'what size class swarm'. Here, it is necessary to obtain information on the swarm as well as on those crabs remaining as infaunal. Simply collecting animals that are swarming will not provide accurate information on the density and size classes within the population.

The fourth issue is 'what proportion of males *versus* females occurs in the population' and 'what proportion of males *versus* females emerges as a swarm'. This requires information on the swarm, the remaining infaunal subpopulation, and the subpopulation prior to swarming. Here again, simply collecting animals that are swarming will provide information on the sex ratio of the swarm, but not accurate information on the sex ratio of the population.

The fifth issue is behavioural variability. This matter is not concerned with static spatial variability in density, which would be addressed through random replicate sampling, but rather the matter of variability in crab behaviour which may result in variation in density of crabs spatially (vertically and laterally) in time, and variability in expression of their ichnological products on the tidal flat surface. This is reflected in behaviour of the crabs where, within the length and breadth of the soldier crab habitat, some crabs may emerge in patches while others create surface workings in patches, and yet others remain inactive.

The sixth issue is 'does the crab population partition with depth with respect to their size classes and to sex ratios'. This issue is not explored in this paper.

The seventh issue is that, at least for *M. occidentalis*, sampling can initiate a "predator avoidance" effect in the species – that is, during sampling, the crab may burrow deeper, and that during low tide while in general it may

reside and be active at depths of 1 cm to 20 cm, it may burrow to depths of 40–50 cm to avoid perceived possible predation. There are indications from descriptions in the literature that other species of *Mictyris* generally behave in a similar manner. As a result, if sampling is too prolonged, coring the upper 20 cm may not retrieve all the animals that were residing under the selected sampling quadrat or core site, and excavating the animals from a quadrat by spade may also induce a "predator avoidance" effect, and cause the animals to burrow deeper than 20 cm, often to depths of 50 cm to avoid collection.

As mentioned earlier, the literature shows that there has been an emphasis in sampling swarming soldier crabs, and a number of studies have not recognised that a proportion of the population, in fact, had remained subsurface, that the sex ratio of the emergent crabs were different to the ratios of those that remained infaunal, and that the size classes also differed between emerged crabs and infaunal crabs. A contrast is the work of Takeda & Murai (2004) who sampled emergent and infaunal crabs, and Rossi & Chapman (2003), who sampled the crabs as infaunal animals.

Sampling methods investigated in this study

Various methods of sampling for soldier crabs are described below according to particular objectives including monitoring of fixed sites, monitoring of areas with pustular structures, depth of occurrence of soldier crabs, and the components of populations dynamics consisting of abundance (subsurface population, and swarms), size classes, and how many replicate samples are required. Most of the work was carried out at King Bay, Dampier Archipelago, however, data from Settlers Beach, near Cossack, and Broome are also included.

Sampling was carried out during a low tide period. It would be possible to sample at high tide using a boat equipped with a Van Veen grab or similar such devices, or using divers and hand corers. However, these latter methods would be logistically difficult and potentially statistically inaccurate with crab numbers likely to be under-represented due to crabs potentially being lower in the substrate to avoid predators during high tide, and more liable to escape collection attempts. Hence sampling during low tides is preferred.

A major problem with sampling on tidal flats, however, is that any excavations by spade, and/or enlargement of excavations around box cores to deepen the sampling, involves interacting with the water table. The water table under tidal flats generally is 10 (-20) cm below the surface during low tide (depending on time of sampling after the tide had receded). As a result, if the walls of the excavation were unsupported, sediment can slump into the excavation and, at all times at depth below 10–20 cm, the material being sampled was a sand/water slurry of varying thixotropy. Crabs normally are relatively mobile in the sand, but this mobility is accelerated when the matrix within which they reside has become a slurry. Also, the slurry itself is dynamic, flowing into excavations and wherever there is a positive hydraulic head, carrying with it crabs entrained in the hydraulic flow (this is particularly the case for juvenile crabs). This is a problem that results in artificial numbers of crabs and artificial occurrence of crabs at depth, as will be described later.

To determine the minimum number of replicate samples required to characterise the density of crab populations by coring, 15 box cores were sampled on 4 sites and the cumulative mean and standard deviation were graphed against cumulative number of cores. These results showed that a minimum of five box cores were required to characterise the density of the population (Fig. 3). From time to time, however, when crab densities were low, 10 or 15 box cores were used. Generally, for cylindrical cores, 15 replicates were used.

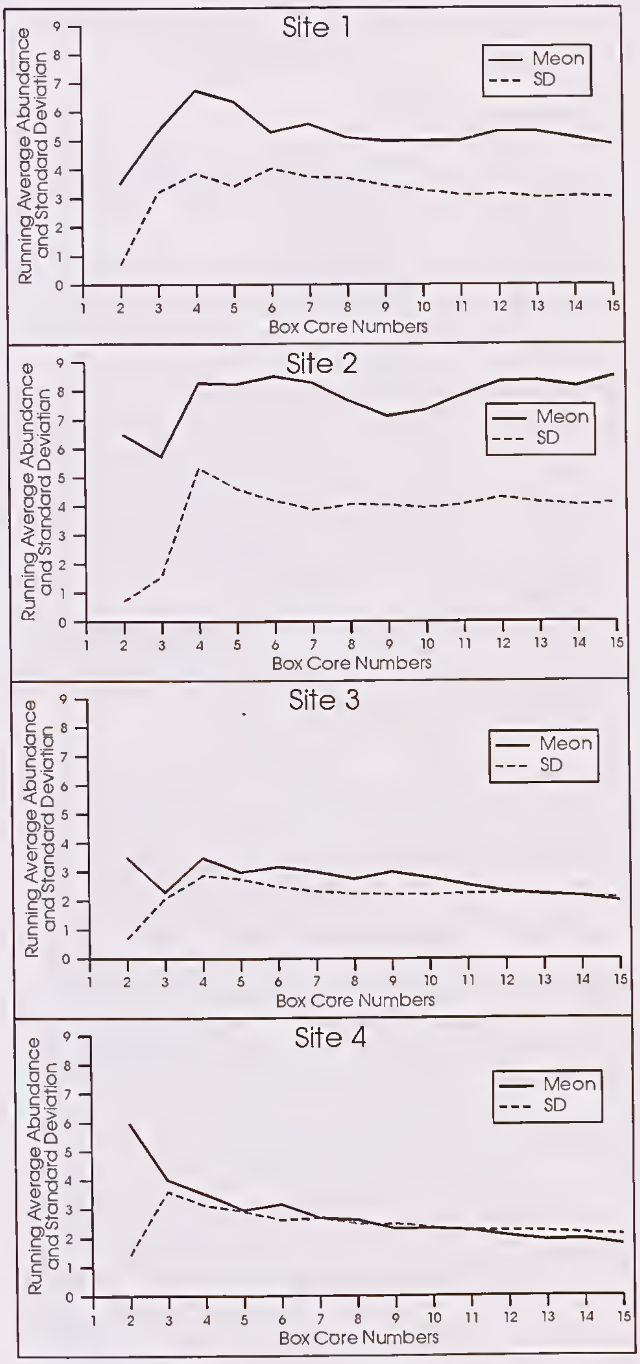

Figure 3. Results of cumulative box core (625 cm^2) sampling showing relationship of mean abundance and the standard deviation to sampling effort.

In all sampling procedures, the sediment retrieved was washed through a 1 mm sieve to retrieve the crabs for counting, measurement, and sex determination. In the earlier part of this study, crabs were returned to the laboratory for measurement. In the middle to latter part of this study crabs were immediately measured in the field and released, or kept and measured over the high tidal period, then released on the next low tide. For crab size, the crab carapace length (Unno 2008) was measured with vernier calipers. Adult soldier crabs exhibit sexual dimorphism and their sex was determined as follows (Unno 2008): male chelipeds are robust and have a large domed tooth on the inner surface of the moveable finger; female chelipeds are more slender and *sans* tooth on the moveable finger; sex can also be quickly determined by gently lifting the abdominal flap to expose either the presence or absence of the male twin peni.

Sampling of fixed sites

Sampling over time within the soldier crab habitat in King Bay, Dampier Archipelago and at Settlers Beach, Cossack (Fig. 1) was generally within a fixed area, marked by posts or position fixing.

The soldier crab habitat in King Bay is reasonably well defined (Unno & Semeniuk 2008). It is a sandy, mid-tidal to high-tidal flat, specifically a sandy ebb-tidal delta located at the mouth of a tidal creek (Semeniuk *et al.* 1982; Semeniuk & Wurm 1987; and Fig. 1 of Unno & Semeniuk 2008). The surface of the habitat is pocked with feeding excavations of stingrays, hence in detail the habitat is undulating, composed of a series of pools and low sand mounds. The sampling sites in King Bay are notated as sites 1, 2, 3 and 4 (Fig. 1B). Within these fixed sites, sampling by 5–15 randomly-located replicate box cores was carried out on consecutive tides, or consecutive days, or separated by two or three days for sites 1, 2, 3 and 4 (Fig. 1B). A two-tailed, unequal variance *t*-test was carried out to assess the significance of the difference of the means of densities of populations determined during different sampling times (with $p > 0.05$).

For some sampling periods at site 4, subsets of this fixed area were sampled, and these were notated as 4A and 4B. Sampling by box cores on a monthly and quarterly basis also was carried out at the fixed sites at King Bay, but this is the subject of a later paper.

The soldier crab habitat at Settlers Beach is the low-gradient mid-tidal to low-tidal sand flat, with sand mounds and shoals and ripples, at the toe of a moderately sloping sandy beach. Within the fixed sites at Settlers Beach, sampling by 10–15 randomly-located replicate box cores or cylindrical cores was carried out.

Sampling of areas with pustular structures

Given that the crab population appeared to be internally mobile, to ensure that crabs were collected within the habitat, in addition to random box cores on tidal flat surfaces (with or without pustular structures), sampling within a fixed area also focused on areas that exhibited pustular structures, *i.e.*, that there was surface evidence of infaunal crabs. Mapping of pustular structures and other crab workings was carried out and this showed that the areas of presence or absence of workings was variable (Figures 8 and 9 of Unno & Semeniuk 2008). The density of crabs under workings also was determined by transect A′-B′ (Fig. 4) where five replicate box cores were sampled every two metres from the centre of an area of workings to an area where crabs appeared wholly absent. The transect A′-B′ shown in Figure 4 crossed the area of pustular workings evident on the morning of 23rd July into the zone where crabs were in the subsurface (but would be producing pustular structures in the afternoon), and into the zone where crabs were absent. The results of sampling for crabs along the transect in Figure 4 for the morning of the 23rd July shows the extent of the crab population, as well as the relationship of crab abundance to crab surface workings, and the occurrence of crabs in the subsurface (but no pustular workings for the morning).

Depth of occurrence

These investigations attempted to determine the vertical range or depth of occurrence of the soldier crab within the substrate as this information is required to ensure that the depth of sampling was sufficient to capture a representative sample of the population.

Three types of sampling equipment were used to determine the depth of occurrence of soldier crabs within the substrate: 1. spade; 2. box core; and 3. cylindrical core. Four types of procedures were used: 1. large blocks of sediment removed by spade; 2. simple extraction of sediment from within a box core; 3. removal of sediment by combined box coring and spading; and 4. simple extraction of sediment from within a cylindrical core.

However, in detail, there were variations within these procedures because, as the sampling was being carried out, it became evident that the crabs responded to the sediment extraction by burrowing deeper. As a result, several types of sampling were undertaken: 1. with a view to sample slowly (*e.g.*, excavate layers in a box core, or layers in a quadrat by spade over several minutes); 2. with a view to sample rapidly (*e.g.*, excavate layers in a box core, or layers in a quadrat by spade within a half minute); 3. with a view to create a disturbance while sampling (*e.g.*, insert cylindrical cores forcibly by hammering); 4. with a view to create a minimal disturbance while sampling (*e.g.*, insert cylindrical cores by quickly and gently vibrating the core into the sediment).

When rapidly sampling sediment from the box cores or quadrats by spade the rationale was to extract the sediment containing the crabs at their natural normal depths as rapidly as possible in order to avoid distortion of results or loss of individuals due to their rapid burrowing deeper into the sediment, or laterally escaping in the subsurface, both in an escape-from-predator response. In these circumstances, with the box coring, cylindrical coring, and spading, the sediment was removed *rapidly* in horizontally layered blocks of 5 or 10 cm thick.

There also appeared to be a natural depth difference in the occurrence of the crabs in relation to tidal flats covered in pustular structures, or tidal flats not yet covered in pustular structures, and in relation to the time involved after the tide had receded and the tidal flat was exposed. As such, sampling was undertaken on tidal flats covered in pustular structures for comparison with sampling on tidal flats not yet covered in pustular structures, and undertaken on tidal flats as soon as the

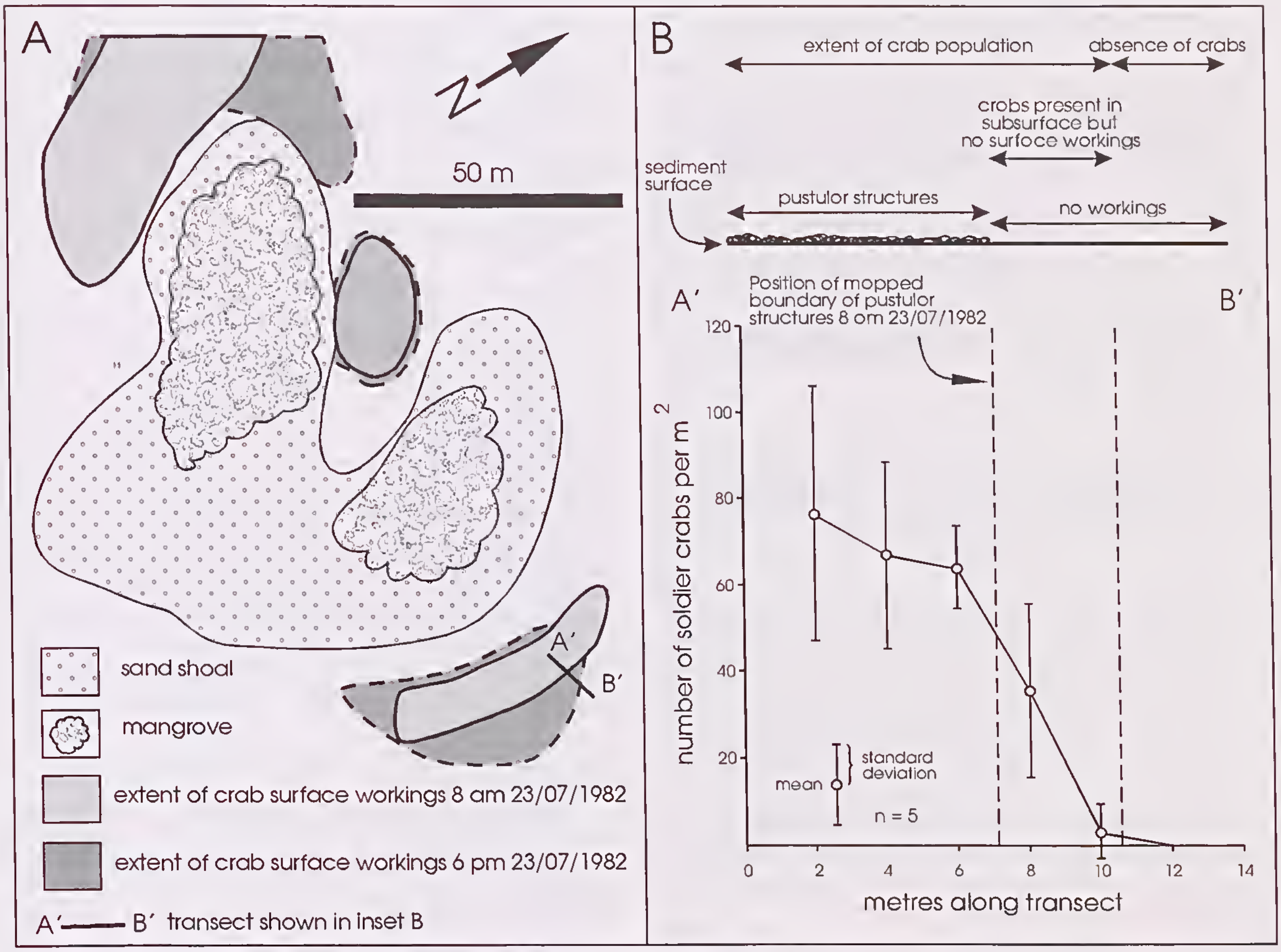

Figure 4. A. Map of the King Bay sampling sites (see Figure 1A this paper; and Figures 1, 8 and 9 in Unno & Semeniuk 2008), and the extent of crab surface workings during the morning and afternoon low tides of 23rd July 1982. B. Results of sampling for crabs along transect for the morning of the 23rd July: extent of the crab population, relationship of crab abundance to crab surface workings, and occurrence of crabs in the subsurface (but no pustular workings for the morning)

receding tide exposed the tidal flats for comparison with sampling on tidal flats hours after the tide had receded.

Since this was not a study of population dynamics and nor a study of the temporal variation in population densities, but of the efficiency of sampling style, box cores, cylindrical cores and spading were not always randomly located on the tidal flat but situated where crab workings were currently or previously evident to ensure that there were crabs in the subsurface. The presence or absence of soldier crab workings were also noted during the investigations. There also was exploration of whether crabs burrowed deeper under areas absent of pustular workings compared to areas with pustular workings.

At one stage, liquid nitrogen also was used to attempt collecting crabs *in situ* within the box core and cylindrical cores (*i.e.*, freeze the crabs *in situ*) to ensure that they did not burrow laterally or vertically, but this procedure was not successful.

Spading: Spading involved the removal of blocks of sediment 20 cm x 20 cm in area by 30 cm deep in two stages – removing a block of sediment 20 cm x 10 cm in area to 30 cm depth, followed by removing the adjoining block 20 cm x 10 cm in area to 30 cm depth. The two blocks of sediment were placed on a table, and squared off to the correct dimensions orthogonally, and then separated into horizontal 10 cm lots which were placed in plastic bags for later sieving. Five replicates using this method were sampled at the one site.

Box coring: Box coring involved use of 25 cm x 25 cm metal box cores, 15 cm, 20 cm, or 45–50 cm deep, inserted fully into the sediment of the habitat. Initially, sediment was rapidly removed with a trowel from the box core in layers of 0–10 cm, 10–20 cm, and for the deeper box cores 0–10 cm, 10–20 cm, 20–30 cm, 30–40 cm, and 40–45 or 50 cm. Later, for more precise determination of soldier crab occurrence in the layers of the vertical profile, the sediment was removed in 5 cm lots for the 15 cm and 20 cm deep box cores, *i.e.*, 0–5 cm, 5–10 cm, 10–15 cm, and 15–20 cm Samples retrieved from a given depth-related 10 cm thick or 5 cm thick layer were placed in a labelled plastic bag for later sieving, so that the subsampling of the box cores could be carried out as quickly as possible. Box coring using the 15 cm and 20 cm deep boxes was undertaken under areas covered in pustular structures, and areas free of pustular

structures (just after the tide receded), and under conditions of rapid removal of sediment *vs* slow removal of sediment. Site 4 was sampled in this manner on a number of occasions between 2002 and 2008, with five replicate samples for each sampling time.

Combined box coring and spading: Combined box coring and spading involved inserting a box core into the tidal flat surface, excavating the content, excavating a moat around the box core, and then pressing the box core deeper, until a depth was reached with sampling when no crabs were being retrieved. The sediment was removed from the box cores progressively in 10 cm lots. This procedure was carried out rapidly and, in a second series of investigation, more slowly.

Cylindrical coring: Cylindrical coring involved three different procedures: 1. use of a 50 cm long PVC pipe with a diameter of 90 mm which was manually and gently vibrated rapidly its full length into the sediment; 2. use of a 50 cm long PVC pipe with a diameter of 90 mm which was hammered its full length into the sediment; and 3. use of a 50 cm long PVC pipe with a diameter of 150 mm which was manually and gently vibrated rapidly into the sediment. The sediment was then extruded from the base of the core in 10 cm lots and sieved. Fifteen replicates using this method were obtained. However, using 90 mm diameter cores involved too many replicates to achieve a sampling area comparable to five replicates of a 625 cm^2 per box core, and later in the sampling programme, the core diameter was changed to 150 mm diameter. This produced unexpected results in that the diameter of the core appeared to have an influence on the depth to which crabs were retrieved (see later).

Sampling populations while crabs were in juvenile stages

When the crabs are in their juvenile stage and wholly infaunal, sampling simply involved box coring or cylindrical coring, using five replicates for box cores and 15 replicates for cylindrical cores. The evidence that there have been no emergent crabs is the pustular surface of the tidal flat with no exit holes evident. Ichnological evidence that adults have emerged, and that some crabs are in the adult phase, includes exit holes, abundant discard pellets, and re-entry rosettes (Unno & Semeniuk 2008).

Sampling populations that were infaunal prior to swarming

When the crabs are at a stage when swarming may occur, estimates of population density cannot be accurately obtained when swarms are active on the surface (because a proportion of the population is still infaunal and a proportion of the population has emerged). In this context, it is important to sample prior to a swarm or after a swarm has fully re-entered the sediment. Soldier crabs tend to form swarms 30–60 minutes after exposure of the tidal flat surface. Sampling for population density, and capturing juvenile crabs, and male and female adults, therefore is best carried out after workings appear on the tidal flat surface, but before the swarming, using five replicates of randomly placed 25 cm x 25 cm box cores with sediment rapidly excavated.

In a given fixed area, the density of a pre-swarm infaunal population may be different to that after crabs have swarmed and reburied, as the adult crabs may have moved on from their site of emergence, but this is the natural temporal variation in density of population to be expected for a vagile infaunal and partly epifaunal, rapidly-moving species.

Sampling swarms concurrently with the subsurface population

Sampling of swarms was carried out by manual collection, harvesting up to ten at a time by scooping up the crabs from the surface, *preferably simultaneously by several collectors to ensure a rapid collection of large numbers of crabs before they re-enter the sediment.* Enough crabs were collected suitable for statistical testing (100 at minimum, and usually several hundred). Efforts were made by collectors to take random samples within their collection area and not bias the sample by collecting only the largest specimens. The use of several collectors is advisable as the crabs, after initially fleeing the collectors, will rapidly burrow into the sediment once a swarm is disturbed. Care was taken not to stampede the swarm over the area of workings which would be the site of the subsurface collection under the swarm. Concurrently with collecting specimens from a swarm, the part of the population which had remained resident under the sediment surface was collected by five replicate box cores.

Once the swarm was collected and individuals measured in the field, the swarm was returned to the site of collection so as not to deplete the population, as sometimes several hundred individuals may be involved.

Results of various sampling methods employed in this study

Monitoring of fixed sites

The sampling within fixed sites of the soldier crab habitat in King Bay on consecutive tides, or consecutive days, or separated by two or three days showed that at times the soldier crab population was relatively consistent in density and sometimes it markedly changed (Fig. 5). The crab population at the fixed sites were relatively consistent in density over the following consecutive days: 23rd and 24th March 1981 for site 1, and 29th and 30th December 2002 for site 3 (df = 24, p = 0.51 and df = 18, p = 0.46, respectively) and over two days for 7th and 9th January 2004 for site 3 (df = 9, p = 0.52). The crab population markedly changed in density over consecutive tides on 1st January 1984 for site 1 (df = 28, p = 0.0008), or consecutive days on 6th and 7th January 2004 for site 3 (df = 8, p = 0.13), and over two to three days over the period 21st and 23rd July 1982 for site 2 (df = 13, p = 0.0004), and 6th and 9th January 2004 for site 1 (df = 9, p = 0.001). At site 3, between the 6th and 9th January 2004, the crab population density changed from 154 ± 80 /m^2 to 313 ± 183 /m^2 to 256 ±34 /m^2, showing the diurnal and inter-diurnal variation in numbers of crabs and the variable patchiness of populations (manifest as changes in standard deviation around the mean abundance).

At the time of these sampling episodes, the structure of the population in terms of size classes remained the

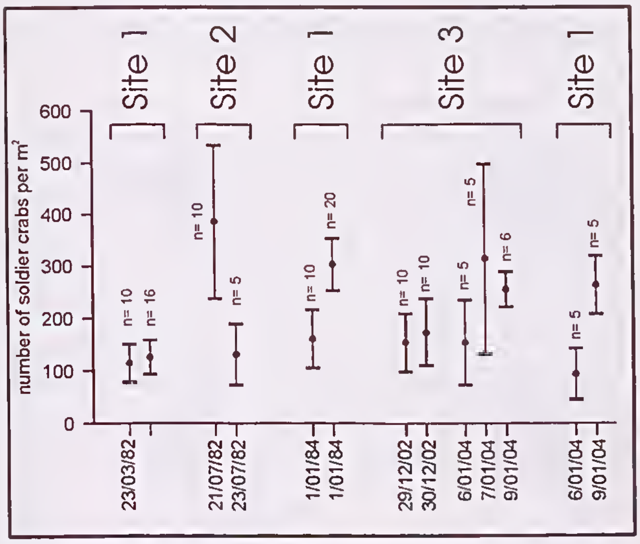

Figure 5. Results of abundance of crabs per m² (mean ± standard deviation) obtained by sampling of sites 1, 2 and 3 (see Figure 1A) over consecutive tides (1st January 1984 for site 1), consecutive days (23rd and 24th March 1982 for site 1, 29th and 30th December 2001 for site 3), or over an interval of two or three days (21st and 23rd July 1982 for site 2; 21st and 23rd July 1982, and 6th to 9th January 2001 for sites 1 and 3).

same, with no influx of juvenile recruits, and so the results for all sites and all times show the variation in abundance and the patchiness of crabs that occur at a fixed monitoring sites over short time frames.

Sampling of areas with pustular structures

The sampling for crabs along a transect grading from those areas with pustular structures to those without pustular structures showed that there were moderate to high numbers of crabs under the pustular areas during a morning low tide, and moderate to low to zero numbers of crabs in the areas free of pustular structures during that same morning low tide. In the afternoon, the area of pustular workings mapped during the morning extended further east by 4 m (Fig. 4). Crabs that occurred in moderate numbers in the subsurface in the morning, but did not produce workings at that time, were to become active in producing pustular structures in the afternoon.

The daily variability in the extent of working of the near-surface of the sediment by crabs to produce pustular structures has been described by Unno & Semeniuk (2008).

Depth of occurrence

Investigations of the depth of occurrence of the crabs using various methods resulted in variation of numbers of crabs between the various methods used. The reader should focus on the percentage occurrence of the crabs in the vertical profile for a given sampling method, *i.e.*, the capture of the crabs as presented by percentage occurrence down the sediment profile.

During the excavation of the sediment layers within a box core, it was observed, particularly for the slow excavations, that the crabs would be burrowing deeper when the layer above them was removed, exposing them, or placing them now in the very-near surface.

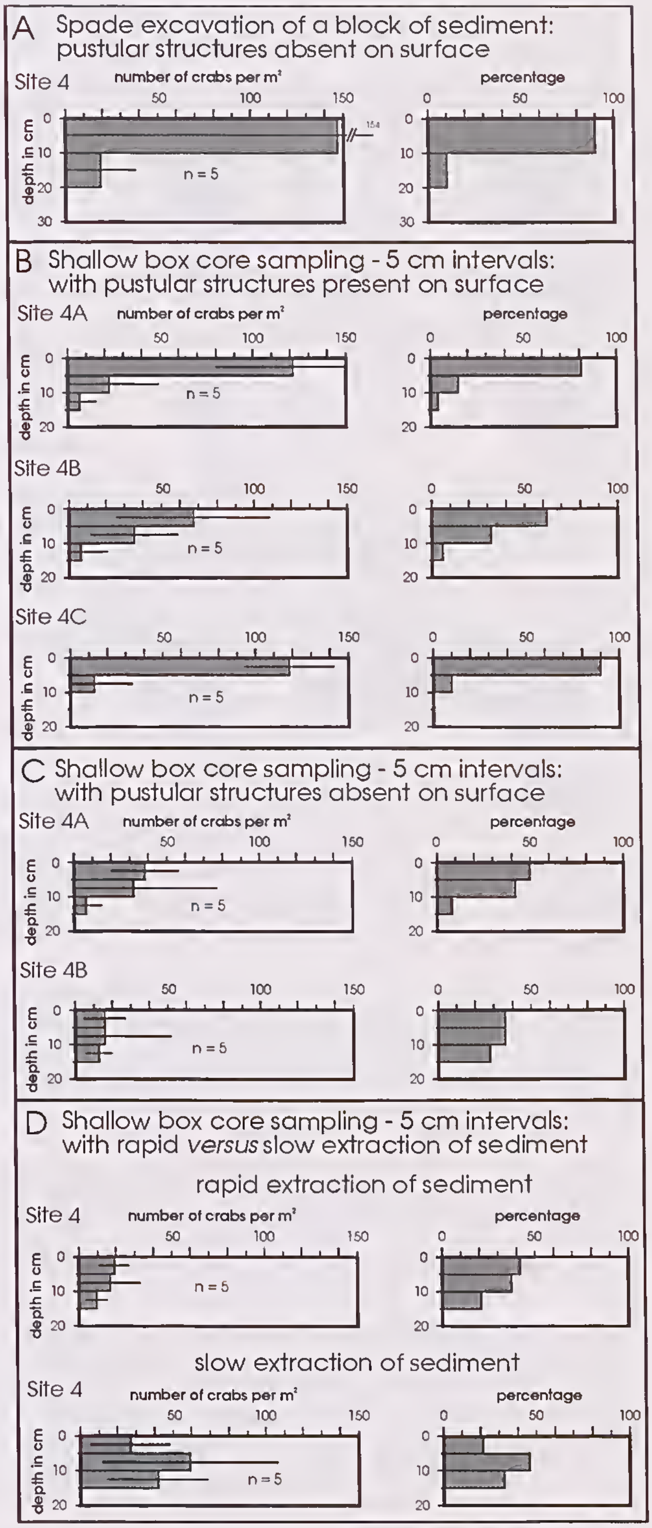

Figure 6. Results of sampling with spading and with shallow box cores to determine depths at which crabs occur under pustular zone and pustule free zones.

The results presented below show occurrence of crabs in 10 cm interval lots, and in 5 cm interval lots. When the results are presented in 10 cm lots, there is not an accurate estimate of the lower depth to which they occur. With 10 cm interval subsampling, where crabs are recorded at depths of 10–20 cm, crabs may not be present wholly over the interval of 10–20 cm, but may be present

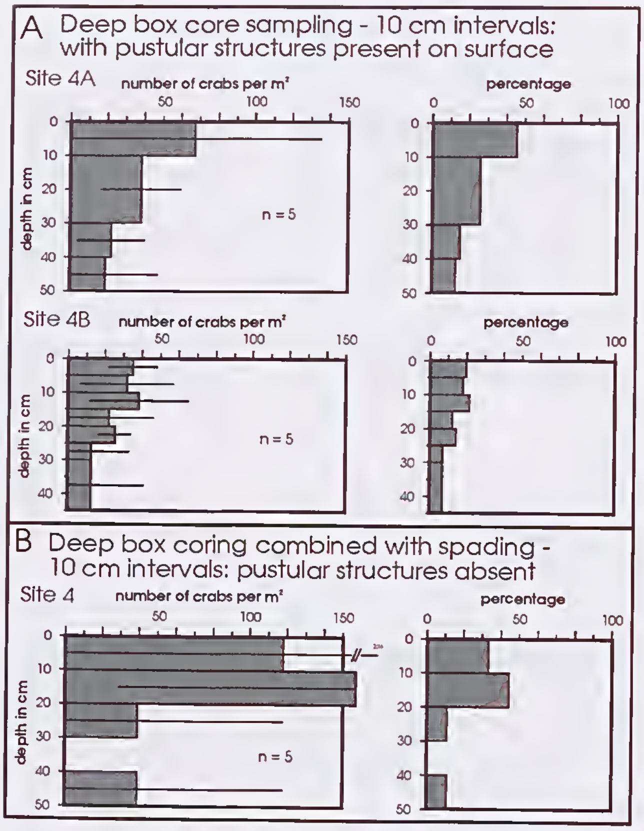

Figure 7. Results of sampling using deep box cores to determine depths at which crabs occur. A. Slow sampling of a deep box core. B. Slow sampling of a deep box core combined with spading.

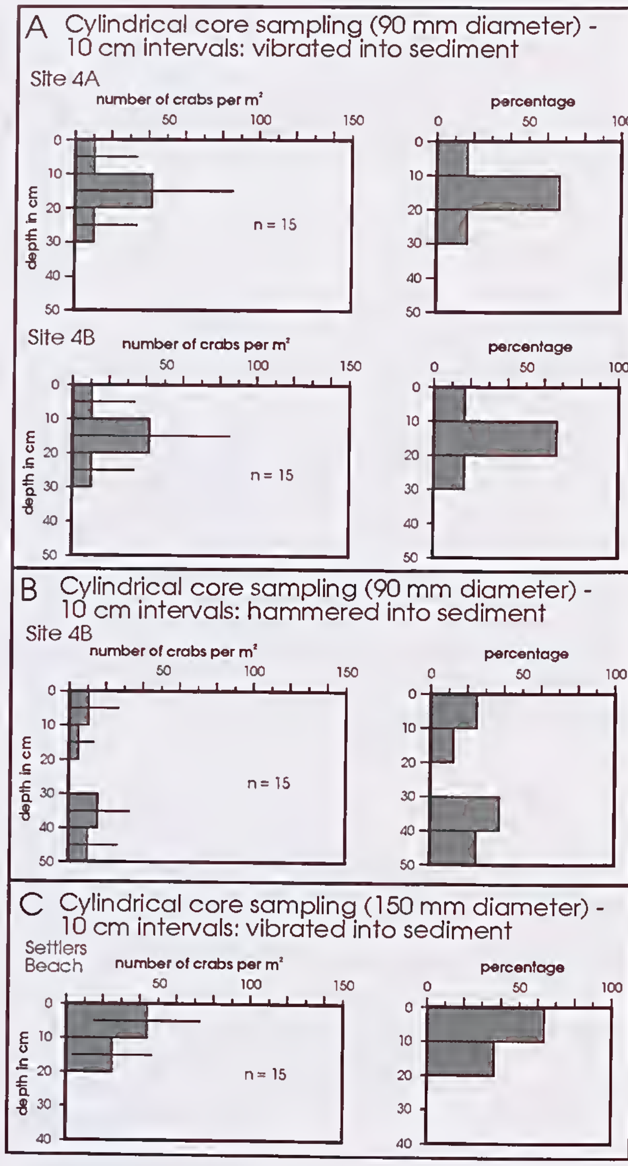

Figure 8. Results of sampling using cylindrical cores to determine depths at which crabs occur . A. 90 mm diameter cylindrical core gently vibrating the core into the sediment. B. 90 mm diameter cylindrical core hammering the core into the sediment. C. 150 mm diameter cylindrical core gently vibrating the core into the sediment.

only to a depth of 0–15 cm – the sampling interval of 10–20 cm may agglomerate the results of *n* crabs between 10–15 cm, and zero crabs between 15–20 cm. The more detailed interval sampling was intended to refine information as to what depth the crabs do occur.

The results of rapid removal of sediment blocks by spading are shown in Figure 6A. The 10 cm intervals of rapid subsampling show the crabs mainly to be confined to the upper 20 cm, and most of these present in the upper 10 cm.

The results from box coring show several patterns. Subsampling of sediment in 10 cm thick layers show that the majority of crabs to reside in the upper 30 cm of sediment, but more refined sampling in 5 cm thick layers showed that the crabs occurred in the upper part of the 20–30 cm level. There is a difference in depth of occurrence of crabs under areas of mats of pustular structures compared to areas where there are no pustular structures (Figs 6B and 6C). The results of sampling site 4B contemporaneously are shown in Figure 6C. Where pustular structures are evident, the crabs are dominantly in the upper 5 cm, and the remainder mostly in the 5–10 cm level. Where no pustular structures are evident, the crabs are still dominantly in the upper 10–15 cm, but more evenly spread in density over the 0–10 cm interval.

There is a difference in abundance and occurrence of crabs with depth with rapid sampling of a box core compared to slow sampling (Fig. 6D). With rapid sampling, denying the crab an opportunity to burrow deeply to escape collection, the crabs are in the upper 15 cm as described above, but more common in the 0–10 cm interval. With prolonged sampling, the crabs were retrieved from the interval 0–15 cm but were more common in the 10–15 cm interval.

The deep box cores penetrating to 50 cm depth showed similar results: the slow excavation of the sediment of a deep box core, with perturbations induced by water table effects and disturbance of the surface sediment, resulted in crabs occurring at deeper layers of the sediment (Fig. 7A).

The combined box coring and spading resulted in two types of results. For rapid sampling, with 10 cm intervals of subsampling, crabs are present in the upper 20 cm. With prolonged sampling, again with 10 cm intervals of

subsampling, crabs are present to depths of 50 cm, as a result of their retreating in front of the descending excavation (Fig. 7B).

The results of the cylindrical coring showed interesting results in that the 90 mm diameter cores, if gently but rapidly vibrated in, yielded results that show that the crabs occur within 30 cm of the surface, while hammering in the core, as would be traditional in some sampling protocols to sample infauna, appeared to disturb the crabs and they occurred to depths of 50 cm (Figs 8A and 8B). In addition, the 150 mm diameter core showed crabs occurring in the upper 20 cm of the sediment profile (Fig. 8C), commensurate with the results of rapid box coring. This would indicate that a narrower diameter tube may be disturbing the crabs while it is being inserted and, in response, they burrow deeper.

These results of investigation into depth of occurrence are summarised in Table 1.

During the subsampling in layers it was observed that there is partitioning of size classes vertically. In general, the juvenile crabs tend to be located at shallow depth, and if crabs are located at 20–30 cm, these tend to be mature adults. This aspect of the population behaviour, however, is the subject of a later study.

Sampling populations while crabs were in the infaunal stage

Soldier crabs, when they are in their infaunal stage (juvenile stages), are the easiest to sample and provide the most simple of results. Though infaunally mobile, juvenile crabs largely are confined to the upper layers of sediment, and hence are readily retrieved by cores or spading. The numbers obtained from sampling reflect what crabs are present in the subsurface and these are mostly restricted to the upper 10 cm of the sediment profile. The variation in density temporally reflects their mobility in the subsurface and their removal by predators.

Sampling populations that were infaunal prior to swarming

The results of sampling populations that were infaunal prior to swarming provides estimates of population density in the habitat. Figures 4 and 5 show density of crabs in pre-swarm situations. Figures 9 and

Table 1

A comparison of the results of the various sampling styles.

Sampling style	Summary of results	Comments
rapid spading of sediment blocks, and subsampling in 10 cm layers	90 % of crabs in upper 10 cm; all crabs within upper 20 cm (Fig. 6A)	rapid sampling on a 10 cm sampling interval indicates crabs present within 20 cm of surface
shallow box cores under pustular structures and subsampling in 5 cm layers – rapid sampling	90 % of crabs in upper 5 cm, > 90 % crabs in upper 10 cm; all crabs in upper 15 cm (Fig. 6B))	pustular structures imply crabs are in the near-surface creating surface-parallel tunnels; the sampling confirms this
shallow box cores under tidal flat free of pustular structures and subsampling in 5 cm layers – rapid sampling	90 % of crabs in the upper 15 cm (Fig. 6C)	lack of pustular structures implies crabs are deeper in the subsurface; the sampling confirms this
deep box cores under pustular structures – slow sampling	< 50 % of crabs in upper 10 cm; all crabs decrease in abundance progressively to 45–50 cm (Fig. 7A)	prolonged sampling allows crabs to burrow deeper in front of the descending excavation
combined box coring and spading – rapid removal of sediment	90 % of crabs in upper 10 cm; no crabs present deeper than 20 cm	indicates on a 10 cm sampling interval that crabs present within 20 cm of surface
combined box coring and spading – slow removal of sediment	~ 40 % of crabs in the 10–20 cm depth interval; crabs continue to be present to depths in the interval of 40–50 cm (Fig. 7B)	prolonged sampling allows crabs to burrow deeper in front of the descending excavation and disturbance
cylindrical core 90 mm diameter rapidly but gently vibrated into sediment	~ 80 % of crabs in the upper 20 cm; all crabs within the upper 30 cm (Fig. 8A)	this sampling suggests that crabs occur to depths of 30 cm
cylindrical core 90 mm diameter slowly hammered into sediment	crabs are dispersed along the length of the core, and are most abundant in the interval 30–40 cm (Fig. 8B)	the disturbance of hammering appears to have caused the crabs to burrow deep and their occurrence over 50 cm may be an artifact
cylindrical core 150 mm diameter rapidly but gently vibrated into sediment	~ 65 % of crabs in the upper 10 cm; all crabs within the upper 20 cm (Fig. 8C)	this sampling suggests that larger diameter cores create less disturbance than 90 mm diameter cores, and the results from the 150 mm diameter cores is commensurate with the results of the rapid box core sampling and the rapid spading; with 150 mm diameter cores crabs appear to be restricted to the upper 20 cm

10 show the size structure of populations prior to a swarm. In comparison to size classes that remain in the subsurface when swarming occurs, it is clear that to obtain accurate estimates of density and of whole-of-population size structure, it is important to sample prior to a swarm.

The sampling of the crabs infaunally also shows their dynamic nature in terms of mobility, and density changes and stability on time-frames that are semi-diurnal, daily, across consecutive days, and over several days (Fig. 5). The abundance of crabs within a fixed sampling site of 5 m x 5 m in their habitat can remain relatively consistent over consecutive days, or change markedly between two tides on the same day, or over consecutive days, or over several days.

Sampling the subsurface population concurrently with swarms

Sampling the subsurface population concurrently with swarms showed that the population is partitioned with respect to size and to gender. Only adults swarm, with the juveniles remaining in the subsurface (Figs 9 and 10). Further, it is dominantly the adult males that swarm.

The results from Settlers Beach show the subsurface population is comprised dominantly of juveniles, and some adults. The adults are dominantly female. The emerged crabs are all adults, dominated by males in the size class 9–14 mm, and dominated by females in the size classes 7–9 mm. Pre-swarm sampling shows that the subsurface population is dominated by juveniles, and where sex could be determined, the population was mixed male and female.

The results from Broome show the subsurface population that remained buried during a swarm was dominated by juveniles, with some adults (mainly males). The swarm was dominated by male adults with some female adults in the 9–11 mm size class.

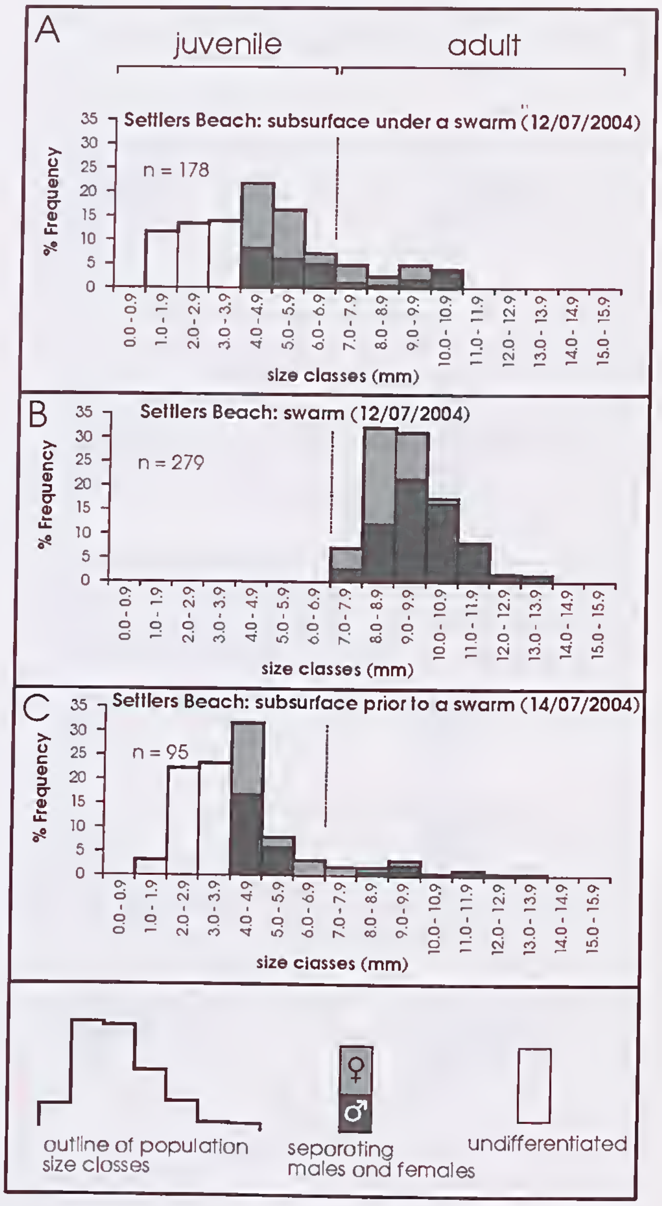

Figure 9. Population structures of soldier crabs at Settlers Beach. The ratio of males to females for a given size class also is shown. A. Population structure of the crabs that remained infaunal during a swarm on July 12th 2004. B. Population structure of crabs that were swarming on July 12th 2004. C. Population structure of crabs as infauna before a swarm emerged on July 14th 2004.

Discussion and Conclusions

The investigation of sampling methods for the Western Australian soldier crab highlighted some difficulties with methods that have been employed elsewhere to date in the general study of the behaviour, population dynamics, population density, and determination of sex ratios of species of *Mictyris*. Notwithstanding that different species of *Mictyris*, when examined in detail, may have varying behaviour and autoecological responses to their environment (as noted in the Introduction), there are many characteristics they share in common (such as swarming, infaunal behaviour, and some aspects of their ichnological products) allowing the principles of this paper to be applicable in a wider generic context. That is, there is enough information in descriptions of the behaviour and population studies of the various species of *Mictyris* and the methods used to study them to indicate that the results of this study have applicability elsewhere, and to compare with the results of this study and to highlight some problems in sampling that have occurred to date.

Generally, soldier crabs have not been perceived to be infaunal, but rather as "crab armies". Many of the studies in terms of population dynamics and determination of sex ratios are carried out only on emergent crabs in swarms, apparently with a perception that the swarms represent the whole of the population (Dittmann 1998, and the initial stages of the work of Takeda & Murai 2004), though there are exceptions to this (*e.g.*, Nakasone & Akamine 1981; Takeda 2005). Consequently, where crabs in a swarm are viewed as representing the whole population, there is no accounting for juveniles and adult females in the subsurface, both of which in fact may numerically comprise the greater proportion of the population. As such, generally, sampling of soldier crabs has not been designed to address the full range of behavioural modes as related to size classes and sex within the population over their life stages.

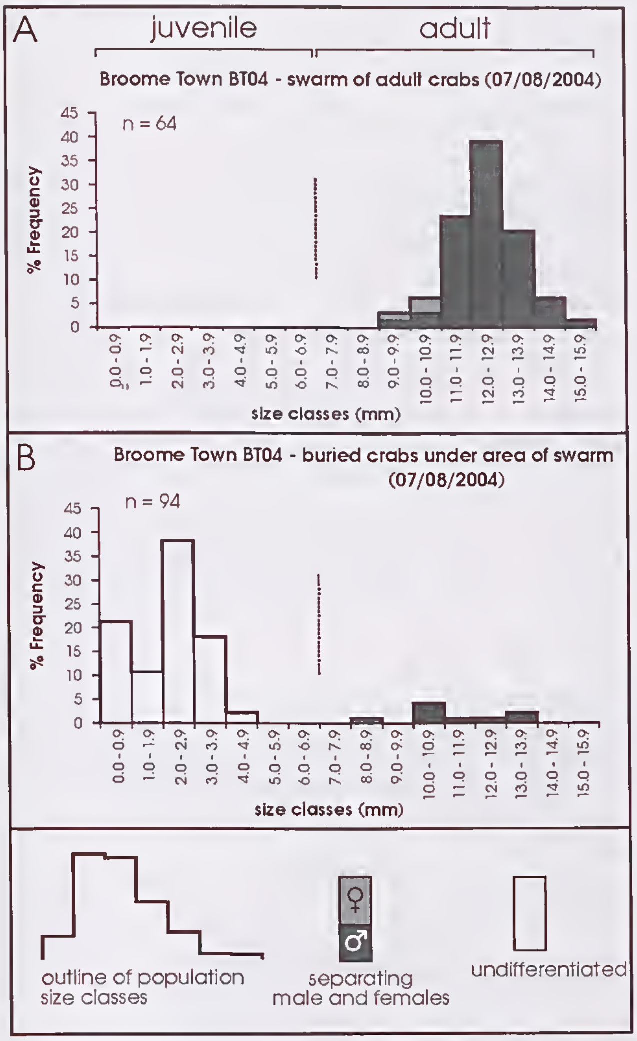

Figure 10. A. Population structures of soldier crabs at Broome. The ratio of males to females for a given size class also is shown. B. Population structure of crabs that were swarming on August 7th 2004. B. Population structure of the crabs that remained infaunal during the swarm on August 7th 2004.

The information deriving from this study and that of Unno & Semeniuk (2008), shows that the Western Australian soldier crab is *largely* infaunal, and emerges only in its late adult stage. Moreover, not all adults emerge for a given swarm. Adult males dominate the swarm with a residual complement of juveniles and female adult crabs remaining in the subsurface. Population studies of soldier crabs need to address the whole-of-population, and thus sampling design has to accommodate the various behaviour of the population as it proceeds through its life stages.

Some of the more specific implications of the sampling results deriving from this study are discussed below.

While many non-sessile organisms on a tidal flat lend themselves to fixed sites for long-term sampling within their habitat because they are not especially mobile or markedly vagile (*e.g.*, species of the crabs *Uca*, *Sesarma*, or *Neosarmatium*, and the thalassinidean shrimp *Upogebia pusilla*, inhabiting relatively fixed or semi-permanent burrows, or worms resident in u-shaped burrows; Lawry 1966, Dworschak 1983, Wolfrath 1992, Emmerson 2001, Layne *et al.* 2003), soldier crabs present themselves as a challenging organism for sampling. While their habitat may be long-term and permanent (for example, the soldier crab habitat in King Bay has been consistently and annually inhabited by these crabs for over 30 years), the soldier crab itself is quite mobile laterally and vertically within this habitat. Sampling for population density will detect fluctuations in abundance that is not necessarily reflecting intra-annual or inter-annual variation in the whole population (resulting, for instance, from local depletion by death or predation, and from regionally-induced recruitment) but rather intra-habitat adjustment and migrations. Thus population density at a fixed site may fluctuate on consecutive tides, or consecutive days, or separated by two or three days (Fig. 11). This factor has to be borne in mind when assessing variation in crab numbers for interpreting population dynamics.

Since the activity of soldier crabs is variable, with workings and/or emergences appearing or not appearing in different locations within the habitat over consecutive low-tidal periods, pustular structures can provide a ready tool for assistance in monitoring a population. The presence of workings is a good indication of the subsurface presence of soldier crabs. However, sampling only where there are pustular structures, and moving away from fixed site areas for monitoring will result in biased sampling. The best approach to obtain a whole-of-population assessment is to map the areas of pustular structures, and then sample in transects across pustular zones to pustule-free zones to obtain an estimate of crab density under the workings *versus* that under pustule-free areas. Estimating density of crab populations needs to involve a process of mapping or delineating the extent that pustular areas are developed and concomitantly collecting crabs by sediment extraction.

Within a fixed site area, the optimum time to sample to estimate population density is after workings have commenced and pustular structures and tunnel structures have appeared on the tidal flat surface. Thus when crabs are nearest to the surface, sampling will ensure that all the crabs under a given sampling quadrat will be retrieved. If exit holes and rosettes are evident, or there are swarms of adult blue crabs, it is too late for sampling the whole population. Approaching a swarm may result in the crabs firstly attempting to run from the perceived predator, and then secondly, rapidly reburying themselves to avoid the researcher and, consequently, the site of coring may have been compromised in terms of natural density of crabs and distribution of size classes. In this context, sampling to estimate the density of the whole-of-population at a fixed site requires pre-swarm sampling.

In the previous studies, it appears that the complex behaviour of the soldier crab in response to sampling procedures also has not been addressed. In this study, different sampling styles resulted in different numbers of crabs being retrieved or different depths that the crab occurred, due to disturbances propagated by the sampling equipment, or the length of time taken to sample, as well as effects due to substrate perturbations during sampling, the effects of a shallow tidal flat water table (on sediment, crabs and sampling), and the water-

saturated sand responding to the excavations and sampling, (*e.g.*, the effects of small-scale hydraulic heads developed during sampling, which can entrain small crabs). The greatest effects or perturbations occur where adults rapidly burrow deeper to avoid the "predator" researcher, or where small juveniles (of lesser specific gravity than, but of the same size as coarse and very coarse sand, *i.e.*, ~ 1–2 mm) are entrained in a slurry. The results are that crabs appear to occur deeper than they would occur naturally; not all crabs may be retrieved, and spurious numbers of juveniles may be incorporated into the sample. To circumvent these problems where there are only abundance estimates, size classes, and sex ratios under a given area required in population studies, the sediment containing soldier crabs should be sampled when pustular structures have appeared (in sufficient density to form a mat) by box cores, or with a = 150 mm diameter cylindrical core (both of which ensure that crabs remain confined inside the walls of the core), or rapidly excavated by spade in a large block (*i.e.*, as a large sediment block removed within 10–30 seconds).

Due to the infaunal and vagile nature of soldier crabs sediment, coring with rapid removal of sediment to address the escape response is suggested as the most appropriate sampling method. Square box cores are preferred to cylindrical cores because of ease of sediment removal. The box cores of dimensions 25 cm x 25 cm surface area and 15–20 cm deep ensure a 95 % probability of collecting organisms with living densities > 0.06 specimens per 1000 cm^3 (Dennison & Hay 1967). Preliminary coring carried out in this study to determine the depth of occurrence of soldier crabs during the low tide period, combined with previous field and aquarium observations (Unno & Semeniuk 2008), suggest that soldier crabs are resident within the upper 10 cm of the sediment. A sampling effort of five spatial replicates will result in a total sample volume of = 46, 875 cm^3. Sediment from cores is removed with hand trowels to be washed through a 1 mm mesh sieve to collect the crabs. While spading produced reasonable results when carried out rapidly as shown in Figure. 6A, in practice, it is the least reliable of the three methods because, if carried out in

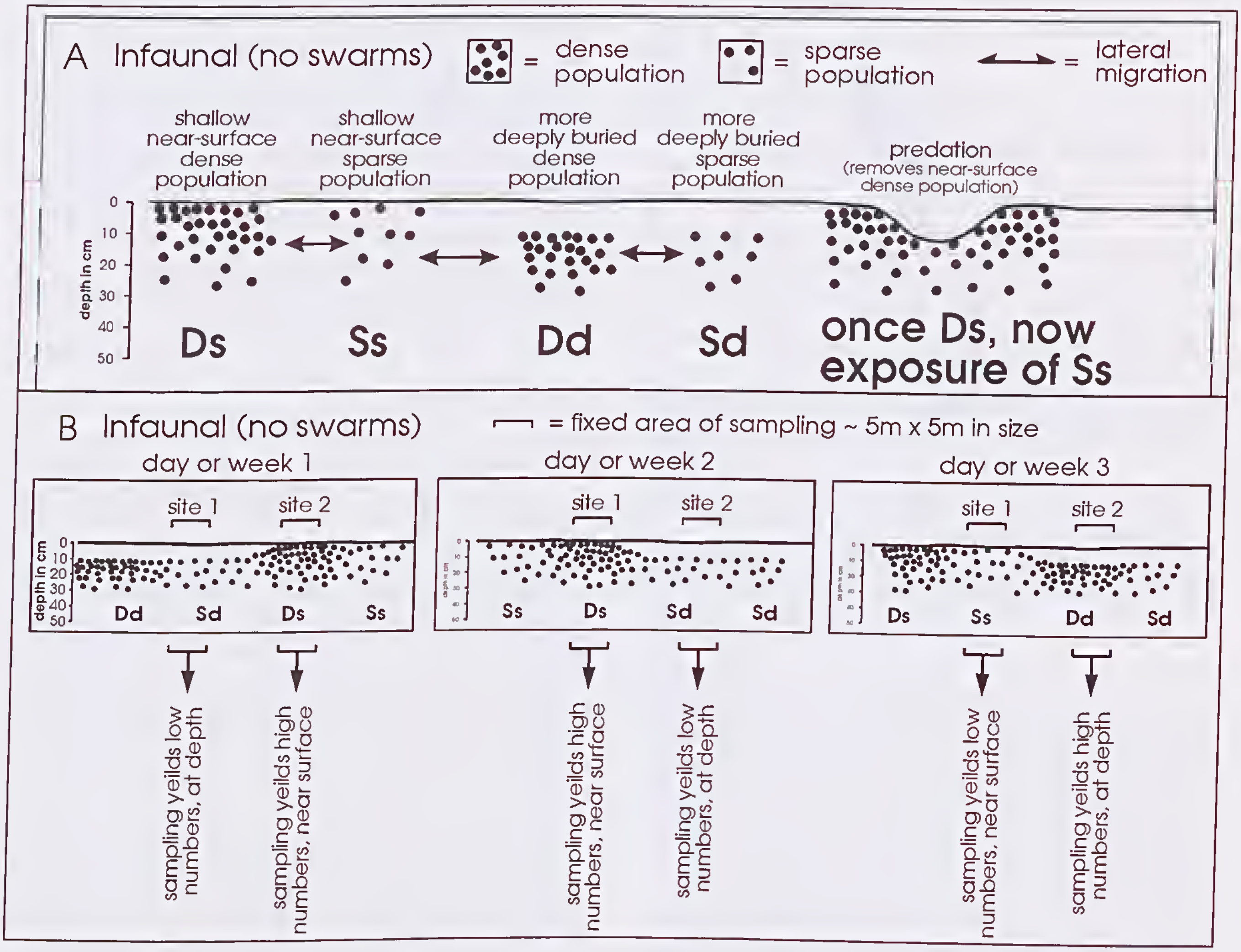

Figure 11. A. Idealised diagram showing the occurrence of dense and sparse infaunal populations of crabs that migrate laterally and vertically, and the effect of predators (that by excavations, expose the deeper occurrences of crabs). B. The varying results of low and high numbers of crabs located at depth or in the near-surface deriving from fixed study sites that intersect the spatially internally dynamic crab population.

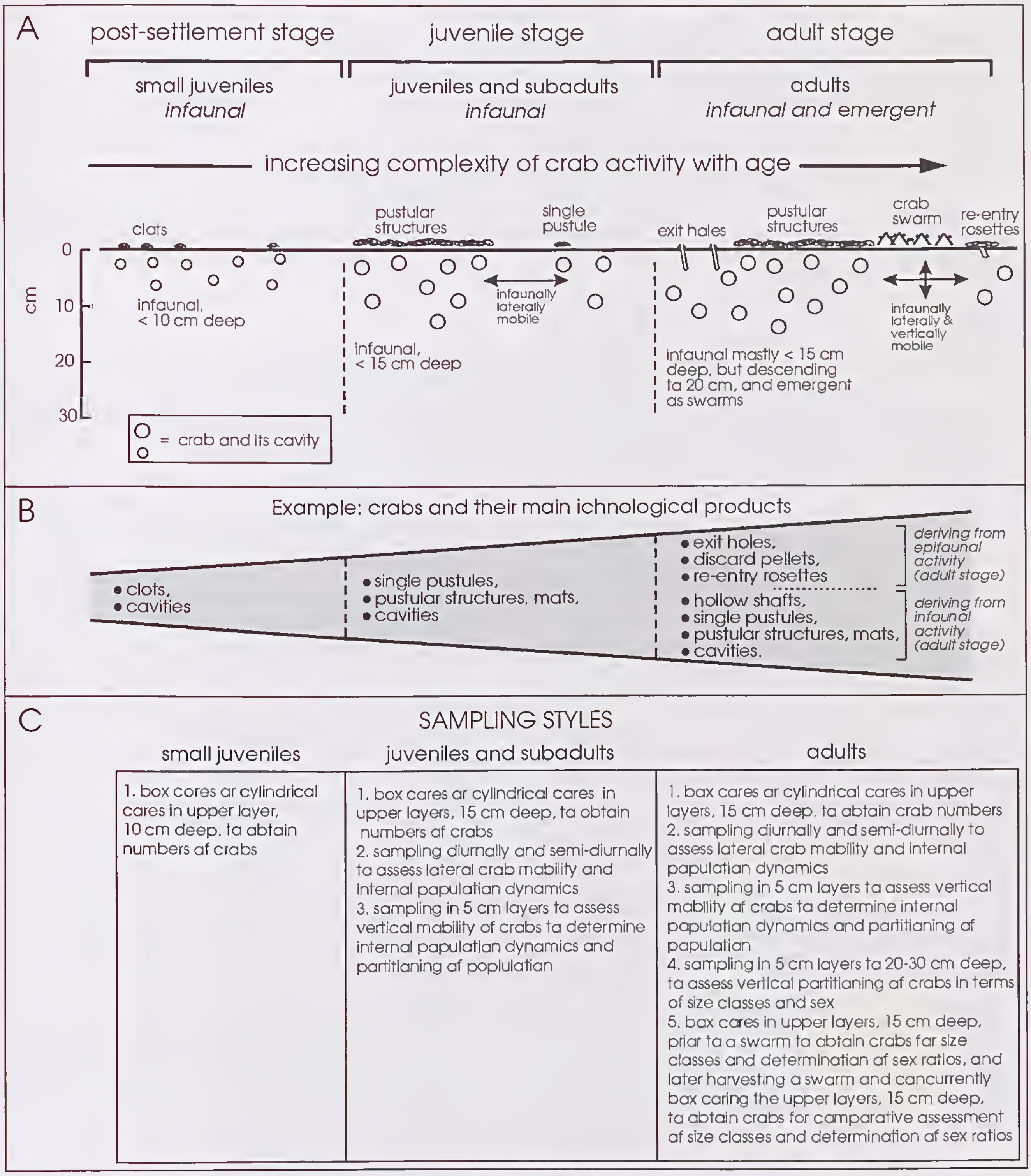

Figure 12. Idealised diagram show increasing complexity of crab behaviour as *M. occidentalis* passes through its life stages, the increasing complexity of information that can be derived and style of sampling required. A. Diagrammatic representation of activities of the soldier crab with respect to its three life stages. B. Example of the increasing complexity of crab behaviour reflected in its ichnological products. C. Suggested sampling that could be undertaken for each of the three life stages.

two stages, there is exposure of a 20–30 cm high wall of sand that is partly submerged by the tidal flat groundwater table, and that has a potential to slump.

The answer to the question of 'how deep does the crab burrow in natural situations?' may be different for the various species of *Mictyris*, and perhaps different for the same taxon in different environments. For the populations in King Bay, it appears to be < 20 cm, and mostly < 15 cm. However, even here, the depth of burrowing changes, depending on whether the crabs are relatively inactive and producing no pustular structures (then they are in the lower part of the interval 0–20 cm), or relatively active and producing pustular structures (then they are in the upper part of the interval 0–20 cm).

Table 2

Suggested investigations and sampling style for the different life stages of the soldier crab.

Infaunal post-settlement juvenile stage

Objective	Suggested methods
depth of burial	determine depth of burial of crabs for a given habitat in a region using box core or cylindrical core, subsampling in 5 cm layers
population density	carry out replicate box coring or cylindrical coring in a fixed site to a depth determined by preliminary assessment of the depth to which the crabs are burying themselves

Infaunal juvenile to subadult stage

Objective	Suggested methods
depth of burial	determine depth of burial of crabs for a given habitat in a region using box core or cylindrical core, subsampling in 5 cm or 10 cm intervals
variation of depth of burial over a diurnal or semi-diurnal period, or a longer period (intra-population vertical migration)	sampling diurnally or semi-diurnally, or over 2–3 days, to determine depth of burial of crabs for a given habitat in a region using box core or cylindrical core, subsampling in 5 cm or 10 cm intervals
population density	mapping pustular structures in a fixed site to assess extent of soldier crab occurrence, replicate coring using box coring or cylindrical coring along transects across the pustular zones into the pustule-free zones (that were determined earlier), to a depth determined by preliminary assessment of the levels to which the crabs are burying themselves
assess intra-population lateral mobility	sampling in a fixed site by box cores or cylindrical cores semi-diurnally or diurnally (*i.e.*, on consecutive tides, or consecutive days), or separated by two or three days
determine partitioning of population in vertical profile in terms of size classes over time of a low-tidal cycle	sampling using box core or cylindrical core, subsampling in 5 cm or 10 cm intervals, from time of first exposure of tidal flat to later high tide inundation
determine partitioning of population in vertical profile in terms of sex over time of a low-tidal cycle	sampling using box core or cylindrical subsampling in 5 cm or 10 cm intervals from time of first exposure of tidal flat to later high tide inundation

Infaunal to emergent adult stage

Objective	Suggested methods
depth of burial	determine depth of burial of crabs for a given habitat in a region using box core or cylindrical core, subsampling in 5 cm or 10 cm intervals
variation of depth of burial over a diurnal or semi-diurnal period, or a longer period (intra-population vertical migration)	sampling diurnally or semi-diurnally, or over 2–3 days, to determine depth of burial of crabs for a given habitat in a region using box core or cylindrical core, subsampling in 5 cm or 10 cm intervals
assessing infaunal intra-population lateral mobility	mapping pustular structures to assess extent of soldier crab occurrence sampling in a fixed site by box cores or cylindrical cores, semi-diurnally or diurnally (*i.e.*, on consecutive tides, or consecutive days), or separated by two or three days
population density in a pre-swarm situation, or population density when the crabs are in a phase of not swarming	mapping pustular structures and ichnological products deriving from emergence to assess extent of soldier crab occurrence replicate coring using box coring or cylindrical coring along transects across the pustular zones to the pustule-free zones, that were determined earlier, to a depth determined by preliminary assessment of the levels to which the crabs are burying themselves repeat sampling semi-diurnally or diurnally (*i.e.*, on consecutive tides, or consecutive days), or separated by two or three days
partitioning of population in vertical profile in terms of size classes, over time of a low-tidal cycle, in pre-swarm situations, or when the crabs are in a phase of not swarming	sampling using box core or cylindrical core, subsampling in 5 cm or 10 cm intervals, from time of first exposure of tidal flat to later high tide inundation
partitioning of population in vertical profile in terms of sex, over time of a low-tidal cycle, in pre-swarm situations, or when the crabs are in a phase of not swarming	sampling using box core or cylindrical subsampling in 5 cm or 10 cm intervals from time of first exposure of tidal flat to later high tide inundation

Table 2 (cont.)

structure of population, in terms of size classes and sex ratios, of the crabs that remained infaunal during a swarm for description and for comparison with the swarm	replicate coring in the area under the swarm, or from where the swarm emerged using box cores or cylindrical cores to determine numbers, size classes, and sex ratios repeat sampling semi-diurnally or diurnally (*i.e.*, on consecutive tides, or consecutive days), or separated by two or three days
epifaunal population characteristics during a swarm for description and for comparision with the crabs that remained infaunal during the swarm	harvesting the individuals during a swarm for determination of size classes and sex ratios

Soldier crabs inhabiting moderately steep sandy beaches, freely and rapidly draining the tidal groundwaters, may burrow deeper than those in King Bay. The imperative before commencing a sampling programme, therefore, is to determine to what depth a given species will burrow in a given habitat for a given region. Effectively, this would be a pilot study of sampling procedures before proper sampling is designed (Principle 5 of Green 1979).

Investigations to determine depth of burial of crabs, and the changes in abundance, or size classes, or sex ratios, vertically (as related to time after low tide, or fall of water table, or day-time *versus* night-time) requires subsampling in layers. This study shows that this can be effectively achieved by rapidly subsampling layers downwards in box cores, subsampling layers from whole blocks of sediment removed rapidly by spade as a single unit, or inserting a cylindrical core extracting it and extruding the sediment from its lower end in 5 cm or 10 cm lots. Where there is investigation of the potential of partitioning of crab size classes and/or sex with depth in the sediment profile, semi-diurnally related to the tides, diurnally, or over seasons, then fine scaled subsampling of sediment layers needs to take place. In all procedures, the sampling and subsampling should be carried out as rapidly as possible. Excavations of large quadrats (*e.g.*, 50 cm x 50 cm or 100 cm x 100 cm), where the sediment is planed off in 5 cm or 10 cm layers runs a risk firstly that where the planed layer is excavated to below the water table the sediment will slurry and be locally mobilised into the quadrat from the wall, or mobilised within the quadrat, thus mixing layers adjacently or vertically by water table effects, and secondly that the crabs will burrow deeper to avoid the researcher " predator", all of which can compromise the results.

Determining depth of burial and that all crabs have, in fact, been fully collected from under a quadrat, or box core or cylindrical core, and that the sample retrieved truly represents a subsample of the population for a given area satisfies Principle 6 of Green (1979).

Given the information above, and the increasing complexity of *M. occidentalis* as it passes through its life stages, a suggested protocol for sampling is shown in Figure 12 and Table 2. The information provided in Table 2 accounts for a range of objectives of any study, and the methods suggested to be employed to document the population features and the population dynamics of the crabs in the various stages of their life cycle. When there are mixed cohorts of the species, the patterns shown in Figure 12 will become more complicated.

Figure 12 suggests that changes in sampling style must follow changes in behaviour effected during the life stages of the crabs, and as the complexity of behaviour and ichnological products of the soldier crab changes, so too the sampling style must adapt, and become more versatile. For instance, soldier crabs in their infaunal juvenile stages are the easiest to sample and provide the most simple of results. These juvenile crabs, though mobile, largely are confined to the upper 10 cm layer of sediment, and hence are readily retrieved by cores or spading. The variation in density temporally reflects their mobility in the subsurface and their removal by predators. Sampling infaunal adult populations prior to swarming, or during the late adult stage when the crabs are in a temporary phase of not swarming, also provides estimates of population density. Such data obtained on population density, whether obtained from juvenile or adult stage crabs will show the dynamic nature of the population in terms of mobility, and density changes and stability on a semi-diurnal, daily, across consecutive days, and over several days. However, when the crabs have matured to the extent that they will swarm, there may be partitioning of the population in terms of size classes and sex both for the complement that emerges and for the complement that remains infaunal. When swarms occur, they are dominated by adult males, with a proportion of adult females and some adult males, and nearly all juveniles remaining in the subsurface, but at this life stage, there also may be some degree of partitioning of size classes and sex in a vertical profile for crabs that remained infaunal during the swarm. Thus, with adult populations with the propensity to swarm, sampling should no longer involve simple coring to collect crabs as it did with juvenile populations, but may have to address a range of complicated patterns to be able to characterise the population in terms of density, size classes, sex ratios, and behaviour.

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Notes on ....

Higher than predicted endurance for juvenile goannas (Varanidae; *Varanus*)

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Abstract. Endurance of juvenile Western Australian varanid lizards was compared with that of conspecific adults. Among adults, endurance generally increased intra-specifically with increasing body size. However, juvenile varanids have a higher than expected endurance. Possible causes for this heightened endurance are discussed, and probably result from a relatively high maximal metabolic rate, as has been previously described for juvenile varanids. Origins of relatively high metabolic rates are unknown, but may be caused by greater oxygen affinity of juvenile haemoglobin when compared to adult conspecifics.

Key words: endurance, locomotion, varanid, lizard

Introduction

Locomotion is considered to be an intermediate step between form and function and is therefore important in ecomorphological and ecophysiological studies (Arnold 1983; Irschick & Garland 2001). Endurance capacity has been studied in relation to both morphological and physiological factors. Many studies have reported that endurance increases with body size (Autumn *et al.* 1994; Garland 1984; 1994), and increases with a higher relative maximal metabolic rate (Garland 1984; Garland & Else 1987; John-Alder 1984). However, few studies have examined whether juvenile lizards conform to this general pattern. We explore this idea for four species of varanid lizard.

Materials and methods

Four varanid species were captured in the field; *Varanus gouldii* (n = 15), *V. mertensi* (n = 11), *V. mitchelli* (n = 7) and *V. panoptes* (n = 12). Each lizard was measured and weighed within two weeks of capture. Snout-to-vent length (SVL) was measured using either digital callipers (± 0.05 mm) for the smaller individuals or with a ruler (± 1 mm) for the large lizards (>300 mm SVL). Mass was recorded using a spring balance or scales. Juvenile lizards were identified by a prominent yolk scar on the abdomen.

We were unable to get large lizards to run at a constant speed on a treadmill. Instead two other measures of endurance were recorded; maximum distance to exhaustion (MAXDIST) and maximum time to exhaustion (ENDUR). Both measures were taken simultaneously by encouraging lizards to run around a circular racetrack. The racetrack was 12.3 m in circumference, 1.0 m in height and 0.8 m in width. Time elapsed for each trial was measured using a stopwatch, and recorded once the lizard was deemed to be exhausted. A lizard was deemed to be exhausted when it received ten taps in quick succession without showing any further forward movement. This stimulus was found to induce escape behaviour in 'fresh' lizards, and partially exhausted lizards. Each individual was run twice and the highest score for each measure of endurance was used. For analysis, both endurance data and size data were log-transformed. The average endurance scores for the juvenile lizards were tested against the 95% confidence interval of predicted endurance, calculated for juvenile SVL by backwards extrapolating the regression for adult varanids (Zar 1998).

As lizards were not run at constant speeds around the racetrack it is possible that these measures of endurance may be the result of both aerobic and anaerobic metabolism, and are therefore not directly comparable to treadmill endurance. However, this measure of endurance is still likely to be ecologically relevant, and is therefore a useful measure of endurance capacity.

Results

When all individuals were included in the analysis for each species, size (SVL) was significantly and positively related to MAXDIST for *V. gouldii* and *V. mertensi* (Table 1). For these species larger lizards ran further and for longer. However, removing juveniles from each data set generally increased the strength of the relationship between SVL and endurance (Table 1).

Table 1

Relationship between body size (snout-to-vent length) with two measures of endurance capacity, maximum time to exhaustion (ENDUR) and maximum distance to exhaustion (MAXDIST) for four species of Australian varanid lizard both including (above) and excluding juveniles (ex. juv.). Bold font indicated P < 0.05.

Species	n	ENDUR		MAXDIST	
		r^2	P	r^2	P
V. gouldii	15	0.01	0.763	0.56	**0.001**
(ex. juv.)	13	0.29	0.054	0.40	**0.022**
V. mertensi	11	0.06	0.469	0.37	0.046
(ex. juv.)	8	0.27	0.190	0.53	0.039
V. mitchelli	7	0.48	0.084	0.19	0.325
(ex. juv.)	6	0.52	0.106	0.72	0.034
V. panoptes	12	0.18	0.174	0.25	0.095
(ex. juv.)	10	0.50	**0.021**	0.31	0.095

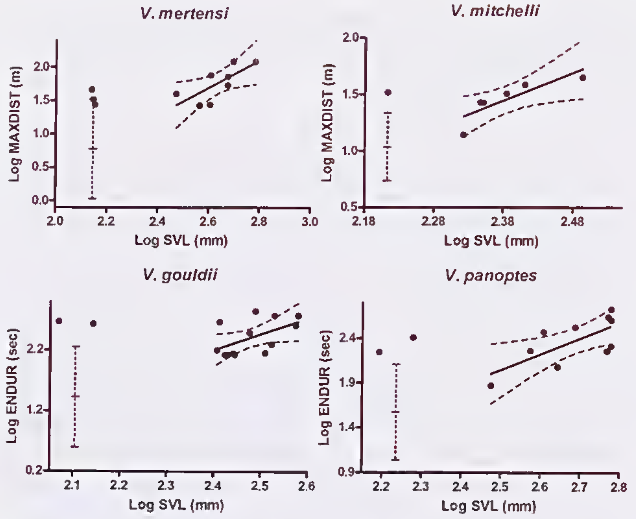

Figure 1. Endurance and SVL for four species of varanid, showing adult and juvenile scores. Regression ± 95% CI shown for regression line of adult lizards. Vertical dashed line shows mean ± 95% CI for predicted endurance of juvenile lizards based on backwards extrapolation of regression for adult lizards. Examples where juveniles have higher than expected endurance are shown. MAXDIST is plotted for *V. mertensi and V. mitchelli*, and ENDUR is plotted for *V. gouldii* and *V. panoptes*.

Table 2

95% confidence intervals of predicted juvenile endurance based on backwards extrapolation of regression for adult varainds. End type – Endurance type, Juv end – Measured juvenile endurance, Pred end – Predicted juvenile endurance based on backward extrapolation of regression for adults, P – significance on one-tailed t-test of measured juvenile endurance vs predicted juvenile endurance.

Species	End type	Juv end	Pred end 95% CI	P
V. gouldii	ENDUR	1.83	1.48 ± 0.48	0.109
	MAXDIST	2.65	1.43 ± 0.83	**0.011**
V. mertensi	ENDUR	1.54	1.04 ± 0.30	0.013
	MAXDIST	2.17	1.65 ± 0.25	0.156
V. mitchelli	ENDUR	1.52	0.77 ± 0.74	**0.046**
	MAXDIST	1.79	1.38 ± 1.12	0.110
V. panoptes	ENDUR	1.75	1.49 ± 0.40	0.129
	MAXDIST	2.32	1.58 ± 0.53	**0.016**

Removing juvenile *V. panoptes* resulted in a significant relationship for ENDUR with both mass and size. Removal of juvenile *V. mitchelli* resulted in a significant positive relationship for MAXDIST with mass and SVL. For *V. mertensi*, it had the effect of strengthening the relationship for MAXDIST with mass and SVL. *Varanus gouldii* was the only exception, showing a slightly weaker (but still significant) relationship for MAXDIST with size after juveniles were removed.

Each juvenile had a higher endurance than predicted from its SVL (Fig. 1, Table 2). Juvenile *V. mitchelli* and *V. mertensi* showed significantly higher endurance when MAXDIST was considered, but not when ENDUR was used. Conversely, juvenile *V. gouldii* and *V. panoptes* had significantly higher ENDUR than predicted from adults, but not MAXDIST. Similar results were obtained when mass was considered.

Discussion

Juveniles appear to have a higher than expected endurance, often higher than lizards many times their size. Why this occurs is unclear. Behavioural motivation is one obvious possibility; juveniles are more susceptible to predation (even by conspecific adults) and are therefore more likely to rely on their flight response. Such a reliance on flight may decline as the lizard grows larger, and predation pressure decreases. However, such an argument might predict a negative intra-specific relationship between mass and endurance for adults, which is not the case. Arguments concerning cost of transport or mass to weight ratios would also fail for similar reasoning.

One problem with interpreting results of this nature was the incomplete data set in relation to mass. There was often a substantial gap in mass between juveniles and the smallest 'adult' of a species. *Varanus mitchelli* had the smallest 'gap' between the juvenile and adults and still showed the characteristic elevated endurance for the juvenile (Fig. 1). This suggests that whatever the mechanism for enhanced endurance in juveniles (be it behavioural, morphological or physiological), it may not be a consistent change throughout development, but works rather like a switch, present only in juveniles but after some event (possibly ontogentically controlled – *i.e.* after the first year/season) it is switched off, and the lizard may not show such great endurance again until later in life (at a much larger size).

What could cause the relatively higher endurance of juveniles? Increased endurance is often associated with increased maximal metabolic rates (VO_2 max) and standard metabolic rates (VO_{2std}; Garland 1984; Garland & Else 1987; John-Alder 1984). Thompson (1996) noted higher VO_2 max and VO_{2std} for juveniles than would be predicted from the intra-specific regression equation for adults, for six species of *Varanus*. The heightened metabolic rate may then explain the elevated endurance score of juveniles.

What causes this heightened metabolic rate remains unknown. One possible explanation may be found in the juvenile cardiovascular system. Frappell et al. (2002) noted that the parameters controlling the transfer of O_2 through the steps of the respiratory system of varanids, seemed to be limited by circulatory convection. This is determined by hemoglobin concentration, O_2 binding capacity of the hemoglobin, and the saturation of hemoglobin. In mammals, fetal blood has a higher affinity for O_2 than maternal blood (Petschow et al. 1978). Similar results have been reported for reptiles. Juvenile alligators have a higher percentage of alkali–resistant hemoglobin than adults (Ramsey 1941). The hemoglobin of embryonic Diamond Back terrapins also has a higher oxygen affinity than hemoglobin of adults (McCutcheon 1947), and similar fetal-maternal difference in the oxygen affinity of blood was observed in viviparous garter snakes *Thamnophis sirtalis* (Manwell 1960). Though

reproductive strategies differ between these groups, it is possible that the blood of juvenile varanids has a similar higher affinity for oxygen than adults. Such an observation would predict that juveniles have a heightened metabolic rate since the limiting factor for the respiratory system will have been reduced, explaining the findings of Thompson (1996) of increased metabolic rates in juvenile varanids. A heightened metabolic rate may then explain the elevated endurance score of juveniles.

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